

# **Multiplicity in Unity**

Plant Subindividual Variation  
& Interactions with Animals

CARLOS M. HERRERA

## **Multiplicity in Unity**

**Interspecific Interactions**

*A Series Edited by John N. Thompson*

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Interactions with Animals*

CARLOS M. HERRERA

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## Preface

Desvarío laborioso y empobrecedor el de componer vastos libros; el de exhibir en quinientas páginas una idea cuya perfecta exposición oral cabe en pocos minutos.

—Jorge Luis Borges, foreword to *El jardín de senderos que se bifurcan*

Values for biological phenomena are often condensed into means. Theoretically, organisms dealing with those values can “expect” the mean value and adapt for it . . . In reality, organisms encounter values one by one, so if variance is high the mean may be irrelevant.

—P. Feinsinger, “Variable Nectar Secretion in a *Heliconia* Species Pollinated by Hermit Hummingbirds”

**M**y interest in the ideas discussed in this book can be traced back to the already remote past when I first became involved in the study of interactions between frugivorous birds and fleshy-fruited Mediterranean plants. Trained as an ornithologist, I was accustomed to using just one measurement to characterize the bill-length phenotype of an individual bird. It struck me as a nuisance that individual fruits produced by the same plant often varied so widely in many important respects, and when I came to characterize the fruit size of a single bush, I had to collect and measure a well-planned subsample of the many hundreds or even thousands of fruits simultaneously available. The same practical trouble struck me again as I shifted to study interactions between pollinators and insect-pollinated plants, this time because I had been taught to consider flowers as the epitome of invariability and constancy. To my dismay, however, flowers also vary, and I had to make repeated measurements on a plant whenever I wanted to properly characterize its floral phenotype. These practical difficulties taught me that, in contrast to the majority of animals, plants generally possess a distinct within-individual component of phenotypic variance that should ideally be taken into consideration.



Later on, as I became more interested in the problem, I also realized that such within-plant variance could be surprisingly large for certain flower, fruit, and seed traits. How, then, to characterize the flower or fruit phenotype of such inconstant individuals? Like others, and for want of a better alternative, I just kept ignoring within-plant variance—sweeping it under the rug, or to be more precise, under the mean, as this is the statistic routinely used to represent (not to describe, to be sure) the phenotypic traits of the reiterated organs produced by a plant. My latest experience regarding within-plant variation, and the one that finally sparked me to write this book, was my discovery that in some species the number of pollen grains on the stigma, and of pollen tubes in the style (two important parameters related to maternal pollination success and the likelihood of microgametophyte competition) are far more variable among the different flowers borne by the same plant, or even the same inflorescence, than among conspecific individuals in the same population. Could there be, after all, some interesting biology hidden behind the familiar nuisance of within-plant variance, routinely brushed under the rug of the mean?

This book addresses this deceptively simple question, paying particular attention to the specific context of plant-animal interactions, as this is the field in ecology with which I am most familiar. Some sparse remarks on the potential significance of within-individual variance in features of reiterated plant structures may be found in the ecological literature of the last few decades, often made from an evolutionary perspective and considering the possible adaptive value of variance. This book, however, purposely follows a different path. Rather than adopting a hypothesis-driven stance and asking from the outset whether subindividual variation in organ traits resulting from the modular architecture of plants is adaptive or not, I start from first principles and leave adaptive and evolutionary considerations for the closing chapter. As will be shown, within-plant variation in organ traits is a universal phenomenon caused by a complex web of mechanisms and with an astounding variety of ramifying consequences, many of which have not been properly acknowledged. In the introductory chapter I briefly define the issue and set the stage. The following chapters examine what features vary among reiterated organs of the same plant (chapter 2), what the magnitude of such variation is in the different types of organs (chapter 3), and how it is temporally and spatially organized (chapter 4). The complex mechanisms, both genetic and ontogenetic, that originate such variation are considered next (chapters 5 and 6). The three sine qua nons for within-plant variation possessing some evolutionary rel-

evance—namely that (1) within-plant variance in organ traits is an individual attribute possessing a genetic basis, (2) animals may respond to such variation, and (3) individual differences in extent and characteristics of variation may translate into differences in plant fitness—are considered in turn in chapters 7 to 9. Finally, chapter 10 provides a synthesis of the possible evolutionary implications of within-plant variation in organ traits.

This book was started in 2003 largely as a spare-time project, and writing has proceeded intermittently since then as time allowed. The order of chapters approximately follows the temporal writing sequence. Although I have attempted to keep an eye on the literature relevant to already-finished chapters, and some colleagues have generously sent articles or drawn my attention to useful references as they have come out, it is possible that some recent investigations relevant to the earlier chapters may have been overlooked. My sincere apologies to those authors whose recent work has been not given adequate credit.

Some of the topics dealt with here have not been specifically considered in earlier experimental or field studies; hence I had difficulty finding relevant published information that could be useful to support or disprove some of the expectations I and others had. There are also very few published raw data that can be used to obtain estimates of variability for different organs and traits, excepting some raw data sets that appeared in print before the habit of compressing data into summary statistics arose. I have had to use my own unpublished raw data or reanalyze published data sets, and to ask colleagues for raw data or analyses not given in their original publications. For their invariably quick and generous responses to my requests, I am deeply indebted to Julio Alcántara, Conchita Alonso, María J. Bañuelos, Raul Bonal, Marisa Buide, Cala Castellanos, Jorge Castro, Cecilia Díaz-Castelazo, Andrew Doust, José M. Fedriani, José L. Garrido, José M. Gómez, Javier Guitián, Pablo Guitián, Benjamin Harlow, Javier Herrera, Asier R. Larrinaga, Antonio Manzaneda, Mónica Medrano, Luis Navarro, José R. Obeso, Víctor Parra-Tabla, Beatriz Pías, Miguel Salvande, Alfonso M. Sánchez-Lafuente, and Pedro A. Tiscar. Conchita Alonso often assisted in locating literature references. Michael Dohm, Alex Kacelnik, and Diana Tomback contributed useful correspondence and discussion, and Fernando Hiraldo provided constant encouragement and removed distracting stumbling blocks as far as he could. José L. Garrido, Javier Guitián, and Pablo Guitián provided accommodation, companionship, and a congenial atmosphere during two stays at the

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## **Subindividual Variability as an Individual Property**

*The Haldane-Roy conjecture is verified and extended: individual plants have not only their characteristic means, but also their characteristic standard deviations and characteristic spatial patterns of within-plant variation.*

In 1959 Indian biometrician Subodh Roy published in *Nature* a one-page note whose succinct title read “Regulation of Morphogenesis in an Oleaceous Tree, *Nyctanthes arbor-tristis*.” Despite its promising title, this contribution actually provided little in the way of information on morphogenesis, as it was exclusively concerned with summarizing the results of a detailed investigation of the variability of the number of petals in flowers of the species, based on the examination of an amazingly large sample consisting of 158,926 flowers (a full account of this and related work was presented in Roy 1963). Roy’s original publication is remarkable not only because of its unbeatable sample size, but also because it has been nearly completely ignored by researchers during the five decades since its publication. It has received only four citations during the period 1960–2005 (according to ISI Web of Science database, accessed February 2006), and I suspect that very few publications appearing in *Nature* will ever equal that record. His obvious failure to arouse interest among peers notwithstanding, Roy was actually a pioneer in attributing seasonal changes in intraplant variability of numbers of floral part to temporally variable homeostasis. He wrote, “The variance of a metrical character may be as important a property of an organism as its mean, and

should be measured on a number of species.” Although his failed appeal to treat variability as another descriptive feature of organisms obviously was aimed at the reiterated, analogous structures produced by plants, it may also be considered a forerunner to the subsequently widespread use of the phenotypic variance of paired structures in (bilaterally symmetrical) animals as a measure of the developmental instability of individuals, a subject discussed in chapter 6.

Roy’s studies of within-plant variation of flowers and leaves in *Nyctanthes*, along with those of Dronamraju (1961) on within-plant heterogeneity in style length in flowers of *Bauhinia acuminata*, and of Davis and Ramanujacharyulu (1971, and references therein) on within-plant variation in the handedness of floral estivation and leaf veneration, were all the direct outcome of one of the new lines of research initiated by J. B. S. Haldane shortly after he settled in India in 1957 (Clark 1968). According to one of his pupils, Haldane initiated this particular research “to understand the nature of organ regulation in living organisms” (Dronamraju 1987), and he clearly placed the results of Roy’s research on within-plant variability of *Nyctanthes* flowers in the context of developmental instability. Referring to these results, and particularly to the fact that within-plant variability in petal number increased toward the end of the flowering period, Haldane (1959, 713) wrote: “If the size of pots made by a potter became more variable at the end of a day, we should say that he was getting tired. I do not know what we are to say about a plant.” In addition, Haldane stressed elsewhere (1957, 312) that “individual plants not only have their characteristic means, but their characteristic standard deviations” and remarked that Roy had taken up “the problem of homotyposis where [Karl] Pearson left it in 1903” (see chapter 2 for the Pearsonian concept of homotyposis). Since this publication by Haldane antedated Roy (1959) by a couple of years, the former is probably to be credited as much as the latter with the paternity of the notion that intraplant variance should be considered as distinctive an individual trait as the mean. For this reason, and because the idea has gone essentially untested since its original formulation, I will refer to it here as the “Haldane-Roy conjecture.” It is interesting to note that the attention paid by Haldane in his later life to the issue of within-plant (or within-genotype, for that matter) variability in organ characteristics denoted a significant shift of opinion about the importance of a phenomenon whose evolutionary significance he had previously categorically dismissed in one of his major works as being “irrelevant for the problem of evolution” (Haldane 1932; see chapter 1

for full quotation). Most likely this change of mind was not unrelated to the increasing significance conferred by some evolutionists during the 1940s and 1950s to the issues of developmental homeostasis and plasticity (Waddington 1941, 1959; Mather 1953; Lerner 1954; Berg 1959).

Haldane's and Roy's suggestion of considering within-plant variances in a given organ trait as another descriptor of the plants' phenotypes in addition to customary trait means (for similar views see Paxman 1956; Suomela and Ayres 1994) was initially motivated by the assumption that observed variability would largely reflect departures from some expected average value due to lack of developmental homeostasis. Nevertheless, characterizing individuals by their within-plant variances still holds considerable practical and theoretical interest even after acknowledging that within-plant variation will in most instances represent the aggregate outcome of a mixture of proximate mechanisms acting simultaneously, and not just the consequence of developmental instability alone, as shown in chapter 6. As noted there, some aspects of within-plant variation probably are an inevitable consequence dictated by direct architectural effects and space constraints (e.g., seed-size variation within cones and conelike fruits). In other cases, however, within-plant variability in organ traits may itself be a trait that has been shaped by special adaptation because it confers some fitness advantage to the plants that exhibit it in comparison to those that do not (Winn 1996a, 1999b; chapter 10). This would apply, for instance, to within-crown variation in leaf traits of trees, such as specific leaf area, nitrogen content, and photosynthetic features (Field 1983; Holinger 1996; Kull 2002).

The possible adaptive significance of within-plant variability in the characteristics of leaves, flowers, fruits, and seeds is discussed at length in subsequent chapters. Nevertheless, before examining the fitness implications of within-plant variability in organ traits, it is essential to verify the generality of the Haldane-Roy conjecture. This implies testing whether, in most species and for most traits of reiterated structures, within-plant variability in a given organ feature is actually a distinctive trait of individual plants, or in other words, whether individual plants in the same population differ with regard to their respective intraplant variabilities. Regardless of their causes, individual differences in variability are the necessary raw material for (phenotypic) selection on variability to occur. The first section of this chapter is devoted to this crucial question. I also consider another facet of within-plant variability that, although it was not incorporated originally into the Haldane-Roy conjecture, does represent a logical

extension of it: Conspecific individuals may differ with regard to the *shape* of their respective trait-value distributions. In addition, plants not only differ in the purely statistical properties of their within-plant trait-value distributions, but also in how such variation is spatially organized at small scales. The second section documents individual differences in the organization of within-plant variation in relation to intrinsic and extrinsic gradients, and in the apportionment of organ trait variance among and within axes of the same plant (e.g., branches, inflorescences). From an evolutionary perspective, individual differences in the statistical properties and spatial organization of within-plant variation would only make sense if they have some genetic component. In the last section of this chapter, I examine several lines of evidence showing that individual differences in the magnitude and characteristics of within-plant variation frequently have a genetic basis.

### **The Haldane-Roy Conjecture Verified**

Since within-plant variability has been very rarely treated before as an individual attribute deserving consideration, there is almost no published evidence that can be used to test the Haldane-Roy conjecture and related notions. Variances or standard deviations for organ traits of individual plants are virtually absent from the ecological and botanical primary literature. For this reason, I rely largely in this section on reanalyses of data from my own studies or those of my associates. Table 7.1 summarizes information on the magnitude and statistical significance of individual differences in within-plant variability of leaf, flower, fruit, and seed traits for those species listed in tables 3.1 to 3.4 with raw data available and sufficiently large sample sizes per plant as to provide reliable estimates of  $CV_{\text{within}}$ . The magnitude of individual differences in variability is expressed in terms of both the observed range of individual plants'  $CV_{\text{within}}$  and the interquartile range, a robust measure of scale. In addition, whenever possible I tested the statistical significance of individual differences in variability by application of a version of Levene's test for comparing relative variabilities (Van Valen 1978).

The data in table 7.1 provide strong and unequivocal support for the Haldane-Roy conjecture for a variety of traits and a sample of species differing widely in growth form and taxonomic affiliation. Regardless of the species and the organ trait considered, and with relatively few exceptions

TABLE 7.1 Variation among conspecific individuals in the magnitude of within-plant variability for leaf, flower, fruit and seed traits.

Trait	Species	Within-plant variability (CV <sub>within</sub> )		Significance of individual differences <sup>a</sup>	
		Range	Interquartile range		
<b>Leaf traits</b>					
Area	<i>Daphne gnidium</i>	12.7–26.9	7.3	****	
	<i>Daphne laureola</i>	24.0–55.1	7.6	****	
	<i>Prunus mahaleb</i>	37.9–77.6	12.2	****	
Fresh mass	<i>Daphne laureola</i>	26.0–51.8	9.9	****	
	<i>Prunus mahaleb</i>	37.8–95.7	10.6	****	
Length	<i>Daphne gnidium</i>	7.3–17.4	4.0	**	
Longevity <sup>b</sup>	<i>Thuja plicata</i>	12.1–37.3	10.2	ns	
Number of teeth in margin <sup>c</sup>	<i>Nyctanthes arbor-tristis</i>	54.1–258.9	147.8	na	
Specific weight	<i>Daphne laureola</i>	5.2–39.7	4.6	****	
	<i>Prunus mahaleb</i>	6.6–30.1	3.4	****	
Water content	<i>Daphne laureola</i>	1.0–9.5	1.5	****	
Width	<i>Daphne gnidium</i>	7.4–17.7	5.7	****	
<b>Floral traits</b>					
Petal number	<i>Nyctanthes arbor-tristis</i>	8.4–11.0	1.7	****	
Petal length	<i>Silene acutifolia</i>	7.7–12.3	2.1	ns	
Corolla length or diameter	<i>Daphne laureola</i>	6.5–23.7	4.1	*	
	<i>Helleborus foetidus</i>	0.4–12.6	2.4	****	
	<i>Hormathophylla spinosa</i>	5.6–12.9	3.0	*	
	<i>Ipomoea wolcottiana</i>	3.1–31.9	7.3	****	
	<i>Lavandula latifolia</i>	1.0–9.3	2.4	****	
	<i>Pancreatium maritimum</i>	1.6–19.0	6.0	**	
	<i>Viola cazorensis</i>	1.2–26.7	6.5	****	
	<i>Epilobium canum</i>	6.5–116.7	na	na	
	Spur length	<i>Viola cazorensis</i>	1.2–26.7	6.5	****
	Nectar production rate <sup>d</sup>	<i>Epilobium canum</i>	6.5–116.7	na	na
<b>Fruit traits</b>					
Transversal diameter	<i>Arum italicum</i>	4.1–13.0	2.8	ns	
	<i>Berberis hispanica</i>	7.2–19.6	4.4	ns	
	<i>Corema album</i>	3.4–11.5	2.2	****	
	<i>Crataegus laciniata</i>	6.2–9.3	1.5	ns	
	<i>Crataegus monogyna</i>	8.4–15.3	4.2	****	
	<i>Daphne gnidium</i>	2.9–12.9	2.9	****	
	<i>Daphne laureola</i>	5.0–8.2	2.1	ns	
	<i>Gonzalagunia hirsuta</i>	5.6–17.8	3.4	ns	
	<i>Guaiacum officinale</i>	3.1–10.8	5.8	*	
	<i>Guazuma ulmifolia</i>	4.9–15.8	4.4	**	
	<i>Hedera helix</i>	5.7–12.1	2.6	*	
	<i>Juniperus communis</i>	5.3–12.7	3.6	*	
	<i>Juniperus phoenicea</i>	5.0–10.5	3.4	*	
	<i>Miconia prasina</i>	5.7–11.9	4.8	**	
	<i>Olea europaea</i>	3.7–7.6	1.0	ns	
	<i>Osyris lanceolata</i>	3.4–10.1	2.1	****	
	<i>Phillyrea latifolia</i>	3.6–10.5	3.2	****	
	<i>Rosa canina</i>	4.8–35.4	3.2	*	
	<i>Viburnum lantana</i>	7.3–12.1	3.2	ns	



Fruit mass	<i>Hedera helix</i>	23.7–34.9	2.1	*
	<i>Juniperus communis</i>	4.0–31.9	9.5	*
	<i>Juniperus phoenicea</i>	16.0–34.8	8.2	ns
	<i>Osyris lanceolata</i>	10.4–57.0	12.9	****
	<i>Rosa canina</i>	12.5–33.2	7.7	*
Seed traits				
Elaiosome mass	<i>Helleborus foetidus</i>	32.4–84.6	14.4	****
	<i>Asphodelus albus</i>	8.2–28.9	7.0	****
Seed mass	<i>Ateleia herbert-smithii</i>	8.5–22.6	3.0	na
	<i>Cassia grandis</i>	7.0–13.0	2.0	na
	<i>Crataegus monogyna</i>	11.3–28.5	5.6	*
	<i>Daphne gnidium</i>	7.2–34.7	7.8	***
	<i>Helleborus foetidus</i>	6.0–51.1	9.1	****
	<i>Ilex aquifolium</i>	15.0–39.1	11.2	****
	<i>Lavandula latifolia</i>	12.6–33.2	10.8	****
	<i>Narcissus longispathus</i>	4.9–20.4	3.9	****
	<i>Paeonia broteroi</i>	5.0–61.0	15.5	****
	<i>Pancreatium maritimum</i>	3.8–59.9	7.9	****
	<i>Phillyrea latifolia</i>	9.4–29.9	8.7	****
	<i>Pinus sylvestris</i>	14.1–20.1	3.6	**
	<i>Prunella vulgaris</i>	28.5–52.8	9.0	na
	<i>Quercus coccifera</i>	7.1–38.6	13.2	***
	<i>Quercus ilex</i>	5.5–28.0	5.7	***
	<i>Smilax aspera</i>	9.2–33.7	6.4	****
	<i>Sorbus aucuparia</i> <sup>a</sup>	11.1–24.2	3.9	****
<i>Tamus communis</i>	8.7–54.2	13.1	****	
<i>Taxus baccata</i>	3.0–23.3	2.4	****	

Note: Estimated with  $CV_{within}$ , as defined in chapter 3. Species and traits are a representative subsample of those listed in tables 3.1 to 3.4, and were selected among those with the largest average sample sizes per plant. Except where otherwise indicated, see those tables for data sources.

<sup>a</sup>Statistical significance of among-individual heterogeneity in the extent of within-plant variation was tested using Levene's test for relative variability (Van Valen 1978). \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; \*\*\*\*,  $P < 0.0001$ ; ns, not significant; na, original data not available for computations.

<sup>b</sup>Data from Harlow et al. 2005; B. Harlow, personal communication.

<sup>c</sup>Data from Roy 1963.

<sup>d</sup>From Boose 1997.

<sup>e</sup>B. Pias and M. Salvade unpublished data.

(10 statistically nonsignificant outcomes out of a total of 62 tests), the tests reveal that conspecific individuals differ significantly in their levels of within-plant variability.  $CV_{within}$  varied considerably among individuals of the same species, as denoted by broad ranges and large interquartile ranges. A within-plant variability continuum occurs in most species, with populations generally comprising phenotypically constant to highly variable plants. This is illustrated graphically in figure 7.1 for four selected examples taken from table 7.1. Within-plant variability ( $CV_{within}$ ) ranged between 38 and 78% for leaf area in trees of *Prunus mahaleb*, between 1 and 9% for corolla length in *Lavandula latifolia* shrubs, between 5 and 20% for seed mass in the perennial herb *Narcissus longispathus*, and between 32 and 85% for elaiosome mass in the herb *Helleborus foeti-*

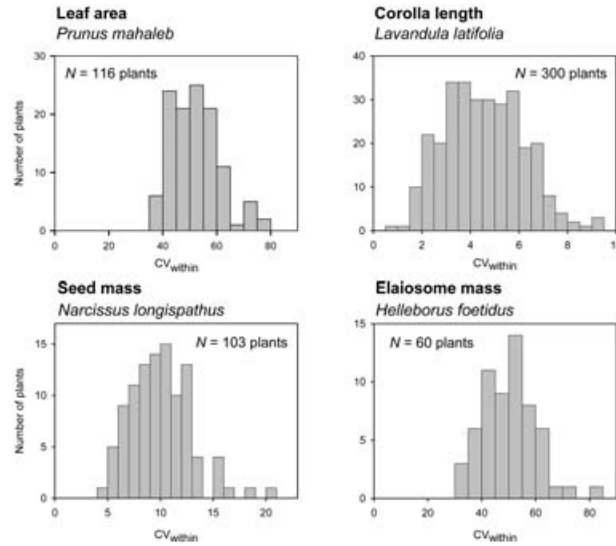


FIG. 7.1 Frequency distributions of within-plant variability estimates ( $CV_{\text{within}}$ , as defined in chapter 3) for representative leaf, flower, and seed traits in southeastern Spanish populations of *Prunus mahaleb* (a tree), *Lavandula latifolia* (a shrub), *Narcissus longispathus*, and *Helleborus foetidus* (perennial herbs). Note differences in scaling of horizontal axes. Data sources are shown in tables 3.1, 3.2, and 3.4 for these species and traits.

*us*. The distributions of  $CV_{\text{within}}$  presented in figure 7.1 are representative of the set of species listed in table 7.1. Regardless of the organ or trait under consideration, therefore, populations of most species are made up of individuals differing widely in the magnitude of within-plant variability in organ traits.

The preceding conclusion is further supported by the few published reports of individual differences in within-plant variability that I have been able to locate. For example, in the nickel-hyperaccumulating plant *Psychotria douarrei*, Boyd et al. (1999) found that individual shrubs did not differ significantly in mean nickel concentration in leaves, but differed widely in the extent of within-plant variation. In *Populus angustifolia*, the magnitude of differences in phenol content among leaves of the same shoot were shown by Zucker (1982) to vary strongly between trees.

For *Lychnis flos-cuculi*, Biere (1991a) reported that seed progenies from different maternal parents sown under controlled conditions differed significantly in their respective coefficients of variation of time to germination. In a population of *Phytolacca americana*, Armesto et al. (1983) found that  $CV_{\text{within}}$  for mean percent germination of seeds, as estimated from germinability of seeds from different racemes on the same plant, varied widely among plants, ranging between 25 and 99%. For *Ipomopsis aggregata*, Pleasants (1983) showed that individual plants differed significantly in within-plant variability of nectar production rate, as measured by their respective  $CV_{\text{within}}$ . In a test of the hypothesis that within-plant variability in nectar production rate increases with the number of open flowers per plant, Biernaskie and Cartar (2004, fig. 1) presented data revealing considerable differences among conspecifics in within-plant variability in nectar production rate. In conclusion, therefore, there is clear support for Haldane's and Roy's suggestion that individual plants not only have their characteristic means but also their characteristic variation around the mean, as well as their contention that subindividual variability should be treated as an individual property in itself. In addition, the fact that different plants in a population show different levels of within-plant variability ultimately implies that the component of population-wide phenotypic variance in an organ trait due to within-plant variation ( $Var_{\text{within}}$ , as defined in chapter 3) is not distributed equally among individuals.

### **The Conjecture Extended: Higher Moments of Within-Plant Distributions**

The Haldane-Roy conjecture ultimately arises from the recognition that all the repetitions of a given organ produced by the same plant in a particular season, or over the course of its whole existence, are not identical. Consequently, a proper description of an individual plant's phenotype with regard to some trait of a reiterated structure will require information on the within-plant *statistical distribution* of organ trait values. This information should include not only the central tendency represented by the mean (first moment of the distribution), but also the scatter around the mean represented by the variance (the second moment). The incorporation of the within-plant variance to the description of individual plant phenotypes represents an improvement in relation to the usual way of describing them using the mean alone. Nevertheless, the variance describes

only the amount of variation exhibited by an individual, yet it is insensitive to possible differences in the shape of within-plant distributions of trait values, an aspect that can also be useful in characterizing individual plants phenotypically. Acceptance of the fact that it is the *statistical distribution* of organ trait values that provides the best and most comprehensive phenotypic description of one individual, rather than any arbitrarily chosen moment of the distribution (traditionally, the mean), opens the way for one obvious extension of the Haldane-Roy conjecture: A complete phenotypic characterization of individual plants would require the inclusion of the third (skewness) and fourth (kurtosis) moments of the within-plant distributions of organ trait values in addition to the mean and the variance.

Skewness characterizes the degree of asymmetry of a distribution around its mean. A positive skewness implies a distribution with an asymmetric tail extending out toward more positive values, while a negative value signifies a distribution whose tail extends out toward more negative values. Kurtosis measures the relative peakedness or flatness of the distribution relative to a normal distribution. Skewness and kurtosis, therefore, are parameters that are informative about the shape of within-plant trait distributions that may provide additional information on individual-level characteristics of variability. Their incorporation represents a logical extension of the Haldane-Roy conjecture. In fact, Roy (1963) explored the possible use of measurements of skewness and kurtosis to characterize differences between plants in the frequency distribution of petal numbers. The question thus becomes: In addition to differing in the means and variances of organ trait values, do individual plants differ also in the shape of trait value distributions?

In practice, incorporating the skewness and kurtosis coefficients (usually denoted by  $g_1$  and  $g_2$ , respectively) of within-plant distributions of organ trait values into the description of individual phenotypes is less generally applicable than incorporating the mean or the variance. It will be statistically feasible and biologically meaningful only if the number of similar structures produced by a plant is large enough for the notion of “shape” of the within-plant distribution to make sense. This limitation will generally restrict the application of  $g_1$  and  $g_2$  to trees and large shrubs producing large numbers of reiterated structures. In these particular cases, however, there is evidence that individual plants also differ in the skewness and kurtosis of their within-plant trait distributions. In nine *Pinus contorta* trees studied by McGinley et al. (1990), two trees showed signifi-

cantly right-skewed seed-mass distributions ( $g_1 > 0$ ), one tree was significantly left skewed ( $g_1 < 0$ ), and the rest did not differ significantly from a normal distribution. These authors did not present numerical data on the kurtosis coefficients, but inspection of frequency distributions in their figure 1 suggests that individual trees also differed in this respect, since some seed-mass distributions departed noticeably from normal-shaped curves by being either too flat (platykurtic) or too narrow (leptokurtic). Comparing the frequency distributions of petal number per flower of *Jasminum multiflorum* plants, Roy (1963) found that some of them had positively skewed distributions, while others had distributions not departing from normality. I was able to compute within-tree skewness and kurtosis coefficients for leaf traits for 116 *Prunus mahaleb* trees with leaf variability data included in figure 7.1 and table 7.1. For leaf area, for example, 32 trees (27.6%) had significantly positively skewed distributions ( $g_1$  range = 0.7–2.0), and 13 trees (11.2%) had significantly leptokurtic distributions ( $g_2$  range = 1.6–8.1), which clearly denotes the existence of considerable individual variation in the shape of distributions for this trait. I obtained results similarly denoting individual variation in  $g_1$  and  $g_2$  for other leaf characters in *P. mahaleb*, and for leaf, fruit, and seed traits of other trees and shrubs included in table 7.1. This lends support to the suggested extension of the Haldane-Roy proposal: In plants producing large numbers of reiterated structures, the skewness and kurtosis coefficients of within-plant distributions could profitably be included as two further descriptive statistics of individual phenotypes in addition to the mean and the variance. In this way, a truly comprehensive statistical description of individual phenotypes could be achieved by combining the first four moments of the within-plant trait distributions.

### **Individual Differences in the Organization of Within-Plant Variation**

Descriptors of within-plant variability based on the moments of trait value distributions are of a purely statistical nature. They provide a numerical description of the magnitude of variation and the shape of the trait distribution, but are insensitive to important biological details, such as individual differences in the distribution over time or space of organ trait values. For a given organ trait, individual plants of the same population not only differ in the amount of variability but also, as shown below, in the nature

of their respective intrinsic and extrinsic gradients of within-plant phenotypic variation. In addition, plants differ in the proportional contribution of variation among and within axes (e.g., stems, inflorescences) to overall within-plant variance in organ trait values, thus giving rise to individual differences in the spatial texture of within-plant variation. In short, individuals differ in how they deploy organ variants over time and space, which means that spatial and temporal patterns of deployment of sub-individual phenotypic diversity should be considered as individual properties too.

### *Leaves*

Several intrinsic and extrinsic gradients of within-plant variation in leaf traits were described in chapter 4. Although these gradients have rarely been examined on a per-plant basis, significant differences between conspecifics have invariably been found in the characteristics of such spatial relationships whenever they have been looked for.

De Soyza et al. (1990) studied the variation of leaf chlorophyll content within eight *Sassafras albidum* trees, and found remarkable individual heterogeneity in the within-plant pattern of variation of that leaf trait. They performed within-tree comparisons between leaves located in the outermost, sunlit shell of foliage (“sun” leaves) and those located near the primary trunk, deep into the crown (“shade” leaves). For all trees combined, sun leaves had higher average chlorophyll content per leaf surface area than shade ones, yet there was considerable individual scatter around this predominant trend: the chlorophyll content of sun leaves was significantly greater than that of shade leaves in five trees, significantly smaller in one tree, and did not differ significantly in two trees. De Boer (1999) studied the variation in pyrrolizidine alkaloid concentration in leaves of *Senecio jacobaea* at different positions along the stem, and reported the data separately for each of four study plants. Alkaloid concentration declined steadily from top to bottom leaves in three plants, but remained fairly constant in one plant. Harlow et al. (2005) demonstrated that, on average, leaf longevity increased significantly with depth in canopy in *Thuja plicata* trees. Individual trees, however, differed significantly in the slope of the leaf longevity–canopy depth regressions. Some trees exhibited very steep relationships while others had flat and nonsignificant relationships. Cowart and Graham’s study of within-plant variation of leaf traits in *Ficus carica* trees (1999) revealed significant plant  $\times$  crown position (inner vs. outer)

and plant  $\times$  height interaction effects on both leaf width and leaf lateral lobe length, which denoted heterogeneity among trees in their respective within-plant gradients in leaf morphology. In a similar vein, Perfectti and Camacho (1999) also reported significant tree  $\times$  exposure effects on leaf size in cultivated *Annona cherimola*. In wild *Prunus mahaleb* trees, water content of individual leaves varies predictably within trees depending on both exposure and height above the ground (fig. 4.2). A detailed analysis of these data on a per-plant basis further revealed significant individual differences in both the exposure- and height-related gradients of intraplant variation in that leaf trait.

### Flowers

Few published reports have explicitly documented individual differences in spatial or temporal patterns of floral features, but these scanty data and some reanalyses of raw data from published studies unequivocally show that conspecific individuals generally differ in their organization of within-plant variation in floral traits. This is apparent, for example, in the significant time  $\times$  maternal family interaction effect on number of ovules per flower found by Mazer and Delesalle (1996) in a greenhouse study of *Spergularia maritima*. In the perennial herb *Pancreatum maritimum*, inflorescences produce four to nine large flowers that open sequentially. On average for the population, corolla length declines with blooming order in the inflorescence, each consecutive flower being on average about 2 mm shorter than the one that opened just prior to it (Medrano et al. 2000, and personal communication). I computed regressions of corolla length on order in the inflorescence separately for the different plants studied by Medrano et al. (2000), and found that regression slopes differed significantly among individuals, ranging between  $-4.6$  mm/position (sequential decline) and  $+2.5$  mm/position (sequential increase). This result denotes broad individual differences in both the sign and the magnitude of the within-plant trend of variation that links flower size with position in the opening sequence. Similar conclusions emerge from detailed investigations of intraspecific and intraplant floral variation in two species of Caryophyllaceae. In *Silene acutifolia*, Buide (2004) found that the number of ovules per flower declined from early (primary) position to later (tertiary) position in the inflorescence, and that this pattern of intrainflorescence variation remained consistent across populations and years of study. To look for possible individual differences, I reanalyzed a subset of Buide's

raw data on a per-plant basis and found that plants differed significantly in the rate of decline in ovule number from primary through secondary to tertiary flowers in the inflorescence. The declining trend was not significant in some plants, and in those in which it was, the slope of the regression varied widely among individuals. Petal length and ovule number also decline regularly from primary to tertiary positions in the inflorescences of *Petrocoptis viscosa* (Navarro 1996, and personal communication). As in the case of *S. acutifolia*, reanalysis of the raw data for *P. viscosa* showed that individuals effectively differed in the slope and statistical significance of the relationship linking floral traits and inflorescence position. A last example of individual differences in the nature of intrinsic gradients of floral variation concerns the perennial herb *Polygonatum odoratum*. Flowers of this species are hermaphroditic, but the number of ovules per flower tends to decline from basal to distal positions along stems, thus exemplifying a clear intrinsic gradient in a floral trait along a plant axis (Guitián et al. 2004). On reanalysis of the original data, I found a significant plant  $\times$  position interaction effect on the number of ovules per flower, the slope of the regression of ovule number on nodal position on stem ranging from  $-1.8$  (acropetal decline) to  $+1.8$  (acropetal increase). Although an acropetal decline in ovule number was the prevailing trend at the population level, a fraction of individuals departed from this general pattern by exhibiting either a reversed trend or no trend at all.

### Fruits

I failed to locate published information allowing for an assessment of individual differences in intrinsic or extrinsic gradients of within-plant variation in fruit traits, either for wild or cultivated plants. Nevertheless, two large unpublished data sets for fleshy-fruited trees from the Iberian Peninsula do reveal that conspecific plants growing in the same population can be surprisingly heterogeneous with regard to the spatial scale at which within-plant variation in fruit traits takes place. *Sorbus aucuparia* is a slender deciduous tree whose fleshy fruits (berrylike pomes) are produced in infructescences located at the tip of branches. Bea Pías and Miguel Salvade (personal communication) conducted a detailed investigation of fruit variation in a large population of this species from the Sierra del Caurel, in northwestern Spain. For each of 44 study trees, they sampled ten ripe fruits from each of five infructescences on different branches ( $N = 2,200$  fruit in total), then measured fruit length and width and counted



the number of enclosed seeds. I did a similar study of fruit variation in the small tree *Crataegus monogyna* in the Sierra de Cazorla, southeastern Spain, in which I sampled and measured ten ripe drupes from each of four branches at main compass directions in 60 trees ( $N = 2,400$  fruits in total). Variance partitions conducted separately for each tree demonstrate that conspecific trees differed widely in the relative importance of differences among and within branches of the same plant as sources of within-plant variance in fruit traits (table 7.2). In populations of the two species, trees where all within-plant variance in fruit traits occurred among fruits of the same branch coexisted with others where most within-plant variance was accounted for by differences among branches. These data demonstrate that, in these species at least, the “spatial texture” of phenotypic variation in fruit traits was also an individual trait, in the same manner as the magnitude of variation or the characteristics of intrinsic and extrinsic gradients.

### Seeds

A number of studies have clearly shown that the spatial organization of within-plant variation in seed traits generally varies among conspecifics. In fourteen plants of *Asphodelus albus* studied by Obeso (1993), mean seed weight declined significantly from basal to distal positions in the inflorescence in ten plants and increased significantly in one plant, and there was no significant position-dependent gradient in seed size in three plants. In *Pastinaca sativa*, average seed weight declines from primary through

TABLE 7.2 Conspecific trees of *Sorbus aucuparia* and of *Crataegus monogyna* differ widely in how the within-tree phenotypic variation in fruit traits maps onto the plant's architecture.

Species and trait	Percentage of within-tree variance due to differences among branches	
	Range	Interquartile range
<i>Sorbus aucuparia</i> (N = 44 trees)		
Fruit length	0–67.9	27.7
Fruit width	0–60.1	25.9
Fruit seediness	0–50.7	20.3
<i>Crataegus monogyna</i> (N = 60 trees)		
Fruit length	0–33.8	11.8
Fruit width	0–78.4	16.1

Note: In both species, individual trees differed widely in the relative importance of differences between branches and among fruits on the same branch as sources of within-plant variance in fruit traits. Based on unpublished data from B. Pias and M. Salvade (*S. aucuparia*) and C. M. Herrera (*C. monogyna*).

secondary to tertiary umbels plants studied, although this pattern is not invariant in all plants (Hendrix 1984). Seeds produced by primary umbels were significantly heavier than those produced by secondary umbels in only nine of the ten plants studied by Hendrix, and seeds produced by secondary umbels were heavier than tertiary seeds in only eight plants. Furthermore, secondary and tertiary seeds' weight relative to primary seeds' weight both varied greatly among plants (ranges = 36–97% and 16–83%, respectively), thus denoting considerable individual heterogeneity in the steepness of the within-plant gradient in seed weight running from primary through secondary to tertiary umbels. For *Onopordum acanthium*, *Amaranthus retroflexus*, *Diploaxis tenuifolia*, and *Tragopogon dubius*, Cavers and Steele (1984) and McGinley (1989) presented data showing considerable heterogeneity among individuals of the same species in seasonal patterns of variation in seed size. To the extent that seasonal variation in seed size in these species reflects architectural effects (chapter 6), these data illustrate individual differences in intrinsic patterns of seed-size variation within-plants. Individual differences may also involve variations taking place at much smaller scales. In *Raphanus raphanistrum*, the pattern of seed-weight variation by position within fruits was shown by Stanton (1984) to differ markedly among maternal families. In three- and four-seeded fruits, for example, seed size declined from basal to distal positions in the fruit in some families, while it did not vary in others.

Evidence from cultivated plants likewise shows that within-plant gradients of variation in the chemical composition of seeds may also differ among conspecifics. Brim et al. (1967) used nuclear magnetic resonance spectrometry to investigate within-plant variation in percent oil content in soybeans (*Glycine max*), and found a significant plant  $\times$  position interaction effect on oil content. The trend of variation in oil content along nodal positions of the stem was not consistent among plants, or in other words, individuals differed with regard to their intrinsic, position-dependent gradients in this seed trait. Working also on soybeans, Marchetti et al. (1995) likewise found that individual plants differed in the characteristics of within-plant gradients in the amount of protease inhibitors in seeds. Similar inconsistencies among individual plants in patterns of within-plant variation in seed mass, oil content, and oil composition have been reported for sesame (*Sesamum indicum*; Mosjidis and Yermanos 1985) and sunflower (*Helianthus annuus*; Fick and Zimmerman 1973).

Individual differences in the spatial or temporal organization of within-plant seed variation may sometimes involve discrete characters. Plants of *Impatiens capensis* produce two types of seeds, originating from

either cleistogamous (CL) or chasmogamous (CH) flowers. In one of his study populations, Waller (1982) found a highly significant plant  $\times$  seed type interaction effect on seed mass, with CH seeds larger in some plants and CL seeds larger in others. This striking result reveals that not only the magnitude, but also the sign of within-plant differences in seed size among seed types may differ among individuals of the same population.

### **Genetic Basis of Differences in Within-Plant Trait Variability**

This section summarizes evidence showing that differences among conspecifics in both the magnitude and the spatial organization of within-plant variation in organ traits often have a genetic basis. Individual differences in within-plant variation represent the realized outcome of the differential operation, importance, or characteristics of one or more of the mechanisms described in chapters 5 and 6, that is, organ-level reaction norms, ontogenetic contingency (phylloclimate-driven variation, direct and indirect architectural effects, responses to biotic factors), and developmental instability. If the factors underlying these mechanisms have a genetic basis, then observed individual differences will ultimately have a genetic basis too. It is not biologically unrealistic to suggest, for example, that individual plants of the same species may differ in the shape of their organ-level reaction norms, degree of physiological integration, three-dimensional arrangement of vascular bundles, density and characteristics of intervessel pits, geometry of fruit walls, homeostatic ability, or any other factor ultimately responsible for within-plant variation in organ traits. To the extent that these structural or functional differences have a genetic basis, then individual differences in the within-plant variation in organ traits caused by these factors will also be genetically based. I consider this indirect evidence in the first subsection below. The clearest evidence of a genetic basis of within-plant variation, however, is provided by a handful of studies considering organ variability itself as another phenotypic trait, and addressing its study by adopting classic quantitative genetics approaches. These investigations are considered in the second and third subsections below.

#### *Indirect Support: Genetic Basis of Factors Causing Within-Plant Variation*

I argued in the preceding chapters that the existence of organ-level developmental reaction norms is ultimately responsible for a significant portion of within-plant variation in organ traits. If individual plants differ

genetically in the shape of their organ-level responses to variation in environmental variables, this provides a mechanism for genetically based variation among conspecifics in within-plant variation. One example of variable organ-level responses to the external environment is the differences between genetically distinct conspecific trees in their leaf-level response curves to variation in the light environment. Within-tree variation in leaf mass per unit leaf area and nitrogen content generally reflect leaf-level plastic responses to variation in the light environment (see references in chapter 4). In *Juglans regia*, genetically distinct lines differ in the functional relationship describing the response of leaf mass per unit area and nitrogen content to variable daily photon flux density (Klein et al. 1991). Intraspecific variation in the magnitude and spatial characteristics of leaf-shape variation along intrinsic plant gradients, such as those involved in heteroblastic species, may also have a genetic basis. In wild *Arabidopsis thaliana* plants, leaves change in size and shape from the juvenile through the adult stage according to a well-defined heteroblastic pattern, and a large number of genes have been identified that influence the developmental pattern that originates such sequential variation in leaf form (Tsukaya et al. 2000; Pérez-Pérez et al. 2002).

The extent and nature of plant sectoriality, another major factor contributing to within-plant variation in organ features, may also differ among conspecific plants, and these differences may have a genetic basis. Löttscher and Hay (1996, 1997) demonstrated experimentally that two genotypes of *Trifolium repens* differed in physiological integration, as revealed by their different capacities to translocate  $^{32}\text{P}$  and  $^{45}\text{Ca}$  from a single nodal root to shoot branches. These genotypic differences were most apparent when treatments were imposed that altered intraplant source-sink relationships (root severance and defoliation). In one genotype the imposed treatments had only minor effects on the translocation of nutrients from the nodal root to distant branches, thus denoting strong sectoriality. In the other genotype, in contrast, the treatments considerably enhanced lateral transport of nutrients to far-side branches, thus denoting weak sectoriality. These differences among genotypes in the extent of sectoriality were consistent with differences in the organization of the vasculature of their stolons. Genetically based differences in the extent of physiological integration (i.e., the inverse of sectoriality) have been also demonstrated for *Fragaria chiloensis* (Alpert 1999) and *Ranunculus reptans* (van Kleunen et al. 2000). These examples involve clonal herbs characterized by vigorous vegetative growth and the formation of large clones, and extrapolate

tions to nonclonal plants such as trees or shrubs should be done with caution. Despite this, they are useful to illustrate that individual differences in sectoriality may have a genetic basis and, therefore, that genetic differences may also lie behind individual differences in the extent and spatial organization of within-plant variation.

Of all the factors accounting for within-plant variation in organ traits, developmental instability has been the only one frequently considered from the perspective of its possible genetic basis. By definition, random deviations from a systematic developmental trend (fig. 6.4) are not heritable, but this is not to say that none of the factors that influence the appearance of such deviations is inherited. The factors that influence the extent of noise at the molecular or cellular level, or those homeostatic mechanisms that correct for errors during development, may have a genetic basis (Palmer 1996). In fact, a few studies using classic population genetics crossing designs have demonstrated significant maternal and paternal influences on the extent of homeostasis in plants. These include studies by Paxman (1956) and Sakai and Shimamoto (1965) on within-plant instability in leaf and floral traits in *Nicotiana rustica* and *Nicotiana tabacum*, respectively, and Bagchi et al.'s study of leaf venation in isogenic lines of *Tectona grandis* (1989). These studies clearly indicate that the fraction of individual differences in within-plant variation in organ traits due to differences in developmental stability often has an heritable component.

#### *Direct Support: Wild Plants*

Traditionally, the level of within-plant variation in traits of reiterated structures has been not considered an individual property worthy of consideration; thus it is not surprising that there have been so few experimental investigations of wild plants that directly look for a possible genetic basis of levels of within-plant variation. The results of the few investigations that I have been able to locate are summarized below, in chronological order. All of them have invariably supported a genetic basis of variability in leaf, flower, and seed attributes.

Paxman (1956) conducted a pioneering investigation of the genetic basis of within-plant variation in leaf and flower traits by means of a set of diallel crosses among five varieties of *Nicotiana rustica*. He treated the within-plant variances of traits as ordinary characters, and then used analyses of variance to detect genetic effects in the usual ways. By this means, he was able to demonstrate significant heritabilities for within-plant

variability in stamen length, pistil length, and leaf-shape index. Half a century later, Paxman's study remains exemplary not only for its insightful dissection of within-plant variation into systematic and random components, mentioned in chapter 6, but also for the elegance of his analytical treatment of results of diallel crosses to demonstrate the heritability of within-plant variation.

In another remarkable study, Seyffert (1983) investigated the genetic basis of within-plant variation in floral anthocyanin content of the annual *Matthiola incana*. The study was based on the analysis of 256 defined genotypes obtained from a full diallel cross of 16 pure lines representing all possible homozygous combinations of four biallelic loci involved in the synthetic pathway of floral anthocyanins. Results demonstrated the existence of a strong hereditary component to levels of within-plant variability in floral anthocyanin content, which were partly attributable to the direct effect on variability exerted by some specific loci and by their epistatic interactions.

Seburn et al. (1990) investigated floral variation in the tristylous aquatic plant *Eichhornia paniculata* by clonally propagating replicates of 14 different genotypes and growing them under common-garden conditions. Populations of this species exhibit considerable variability in floral traits, including the number and symmetry of tepals, and the degree of filament elongation in short-level stamens. In addition to the ordinary question of whether genotypes differed in mean floral traits, these authors also investigated whether they differed in the amount of floral variability. Overall within-genotype floral variability, as measured with the determinant of the trait covariance matrix, exhibited extreme variation among genotypes, thus demonstrating a genetic basis of intraplant variation in floral traits in this species.

Biere (1991a) used a full diallel crossing design to analyze the genetic basis of variation in time to germination among seeds of the perennial herb *Lychnis flos-cuculi*. Genotypes obtained from controlled crosses differed significantly in the variability of germination time exhibited by their seed progeny, the coefficients of variation of time to germination ( $CV_{\text{within}}$ , as used in this book) ranging between 31 and 72%. High or low  $CV_{\text{within}}$  values of maternal progeny mainly resulted from variability within each full-sib family and not just from variation among the full-sib families from a common female parent sired by different paternal parents. Differences between genotypes were statistically significant, as revealed by comparisons of the  $CV_{\text{within}}$  between pairs of progeny groups from different mater-

nal genotypes, thus denoting the genetic basis of within-progeny variability in time to germination.

Winn (1996a) investigated the genetic basis of within-individual variability in leaf traits for the annual *Dicerandra linearifolia*. Plants from 24 paternal half-sib families were raised in growth chambers, and five leaf traits (area, thickness, chlorophyll concentration, chlorophyll *a:b* ratio, density of stomata) were measured for two leaves produced by each plant at different times in the seasonal cycle. There was significant within-individual variation in four of the five traits examined. Individuals differed in the magnitude of within-plant variation in leaf traits, and there was additive genetic variation for within-individual variability in leaf area, chlorophyll concentration, and chlorophyll *a:b* ratio.

#### *Direct Support: Cultivated Plants*

As already noted on several occasions in this book, intraplant variation in the characteristics of reiterated structures of economic value (e.g., fruits, seeds) has traditionally been a matter of concern to agronomists, fruit growers, and farmers in general, who have long endeavored to reduce this unwanted source of heterogeneity in crop products. This has prompted a considerable number of breeding efforts to develop cultivars or synthetic lines characterized by reduced within-plant organ variability. Published examples abound for cultivated plants grown under controlled uniform conditions demonstrating a genetic basis of differences in both the magnitude and the spatial organization of within-plant variation. I will not provide here a comprehensive review of the extensive literature available, but only a summary of representative examples.

Different clones or cultivars of the same species often differ characteristically in the magnitude of within-plant variation in organ traits, which clearly points to a genetic basis of such variation. Three poplar (*Populus*) clones studied by Casella and Ceulemans (2002), grown under uniform conditions, were similar in exhibiting vertical variation in leaf mass per unit area and leaf nitrogen concentration, but differed widely in their ranges of variation. For leaf fresh mass per unit area, for example, the within-clone ranges were 175–275, 150–425, and 175–400 g/m<sup>2</sup>. In 17 poplar clones studied by Pellis et al. (2004), the degree of heterogeneity of leaf area along single shoots was a characteristic feature of each clone, and the coefficient of variation of leaf area within the same shoot ranged widely (37–86%). In sunflower (*Helianthus annuus*), the coefficient of variation of the oil

content of single seeds within sunflower heads differed among varieties, and there was a significant variety  $\times$  position effect on fatty acid composition of oil seeds, revealing that the spatial pattern of within-head variation in oil composition was not consistent across varieties (Zimmerman and Fick 1973). In oats (*Avena sativa*), seed-size variability and the shape of seed-size distribution depended on genotype (Doehlert et al. 2004). And in *Brassica napus*, the  $CV_{\text{within}}$  for the protein content of single seeds varied among plants depending on cultivar (Velasco and Möllers 2002).

Differences between cultivars, varieties, or isogenic lines of cultivated plants in the spatial organization of within-plant variation in organ traits are also indicative of a genetic basis. In *Nicotiana tabacum* the pattern of variation in leaf size along nodal positions in the stem varies considerably among varieties, with some varieties producing the largest leaves at intermediate positions and others at the most basal nodes (Sakai and Shimamoto 1965). The poplar clones studied by Casella and Ceulemans (2002) mentioned earlier not only differed in the magnitude of within-plant variation in leaf features, but also had characteristic, clone-specific vertical profiles of variation in leaf traits. Volatile terpenoid levels and composition in root and leaves of carrot (*Daucus carota*) are under genetic control (Simon 1982; Kainulainen et al. 1998). In a study of four genetic stocks of carrot, Senalik and Simon (1987) demonstrated that the content and composition of volatile terpenoids varied among roots and leaves of the same plant, and among different parts of leaves. Although these authors did not perform explicit analyses to test for genotype differences in the spatial pattern of terpenoids, their graphs clearly show that the within-leaf pattern of terpenoid emission was specific to each genotype. The amount and composition of the terpenoids emitted by the petiole, midrib, and leaf blade were similar in some genotypes but differed considerably in others. Habegger and Schnitzler (2000) further showed that the fine-scale pattern of intraleaf terpenoid distribution in carrot was cultivar-specific.

Studies of cultivated fruits and grain crops also reveal that differences in spatial patterns of within-plant variation in fruit and seed traits can be genetically based. The size of ripe tomato fruits (*Lycopersicon esculentum*) varies depending on position on the plant, and the relationship that links fruit size and nodal position varies among cultivars (Bertin et al. 1998). A similar contrast was documented by Rajala and Peltonen-Sainio (2004) for two oat (*Avena sativa*) cultivars, which exhibited different patterns of within-panicle variation in seed size. While in one cultivar seed weight declined only slightly from the primary to the secondary positions



in the panicle, the intrapanicle gradient was quite steep in the other cultivar. In perennial ryegrass (*Lolium perenne*), different genotypes exhibit distinct intrinsic gradients of seed-size variation with position in the inflorescence (Warringa, de Visser, and Kreuzer 1998; Warringa, Struik, et al. 1998). Certain varieties of corn (*Zea mays*) exhibit position-dependent variation in the fatty acid composition of seed oil along the ear, while others do not (Jellum 1967). A significant variety  $\times$  flower position effect has been reported for seed oil content in *Carthamus tinctorius* (Williams 1962), denoting that intrinsic within-plant gradients of seed variation were variety-specific. Calderini and Ortiz-Monasterio (2003) studied the effects of position in the spike on the macronutrient and micronutrient concentration of wheat (*Triticum aestivum*) grains. They compared patterns of seed chemical variation along spike positions in two cultivars and one synthetic hexaploid line, and found significant genotype  $\times$  position interaction effects on Ca, K, P, and Mn concentration, demonstrating that genetically different lines exhibited contrasting intrinsic gradients of seed chemical composition along the spike. Similar results were obtained by Bramble et al. (2002) in a comprehensive study of the variance structure of single-grain protein content in four wheat cultivars in western Kansas. In addition to other sources of variability (e.g., field, plot), these authors evaluated the relative importance of variance among spikes within-plants, among spikelets within spikes, and among kernels within spikelets, as sources of variation in the protein content of seeds. Cultivars differed in the nature of within-spike gradients in seed protein content, and each of them had a characteristic spatial structure of within-plant variance in the trait under consideration.

Possibly the strongest evidence of a genetic control of differences in within-plant variation in seed traits has been provided by studies of variation in the size and characteristics of rice grains. Individual rice grains located at different positions in the panicle differ predictably in size and in their amylose and starch content (chapter 6), and within-inflorescence patterns of seed variation are cultivar-specific (Zhang et al. 2003; Liu et al. 2005), which clearly points to an underlying genetic basis. Direct supporting evidence was provided by Jeng, Wang, et al.'s study of wild type cultivar Tainung 67 and its artificially induced mutant SA419 (2003). The two cultivars showed different starch and amylose accumulation patterns in relation to grain positions on the panicle. In the wild type cultivar there was a decline in amylose and starch accumulation in the grains located on proximal secondary branches in comparison with grains located on distal

primary branches. In the mutant cultivar SA419, in contrast, grain position had little effect on the contents of starch and amylose of grains located on different branches, which clearly demonstrated that differences between cultivars in patterns of within-plant variation in seed characteristics are genetically based.

### Summary and Closing Remarks

The evidence presented above documents two aspects that are fundamental to the analysis and interpretation of the ecological and evolutionary significance of within-plant variation in organ traits to be undertaken in the following chapters. On one hand, conspecific individuals ordinarily differ in the extent and spatial organization of intraplant variation in phenotypic traits of reiterated structures. On the other, there is compelling evidence that these individual differences in magnitude and organization of variation are genetically controlled. Verification of the Haldane-Roy conjecture, and its reinforcement by indications of a genetic basis of within-plant variation, should impel us to change the ways in which we characterize individual plant phenotypes. Almost without exception, this has been traditionally accomplished by using exclusively the mean of a sample of organ trait values (e.g., in phenotypic selection studies or investigations of geographical variation). If individual plants not only have characteristic means but also characteristic standard deviations, then some measure of intraplant variation (e.g., variance, standard deviation) or relative variability ( $CV_{\text{within}}$ ) should routinely be used in addition to the mean to properly characterize individual plants' phenotypes with regard to organ traits. In other words, the within-plant variance should be granted a descriptive value of the phenotype similar to the value traditionally conferred on the within-plant mean of organ trait values.

Acceptance of the Haldane-Roy conjecture opens the way to examining variation among characters, among species, or among populations of the same species, also from the perspective of their levels of within-individual variability. Statistically significant individual differences in variability are not universal. Real and Rathcke (1988), for example, found no differences among *Kalmia latifolia* shrubs in levels of relative variability in per-flower nectar production rate, and not every example listed in table 7.1 exhibits significant individual differences in variability. Identifying patterns and ecological correlates of interspecific variation in the magnitude of individ-

ual differences in variability will contribute to our understanding of the selective pressures ultimately responsible for that variation, as discussed in chapter 10. Patterns of geographical variation and regional phenotypic differentiation within species may also be examined from this perspective. Geographical variation in flower, fruit, or seed traits, for example, has invariably been addressed from a mean-centered perspective. Investigations of geographical variation in floral traits have traditionally proceeded by first characterizing each individual plant by its mean value for the phenotypic trait of interest (e.g., corolla length), and then examining differences between regions or populations in these plant means (e.g., Herrera et al. 2002; Herrera, Castellanos, and Medrano 2006). But recognition of the fact that within-plant variability is another trait of individuals should lead us, when investigating geographical variation, to consider the possibility of population differentiation in that trait and not only in the mean. This essentially unexplored aspect of population differentiation is illustrated in figure 7.2 for 15 southeastern Spanish populations of the shrub *Lavandula latifolia*. For these populations, Herrera, Castellanos,

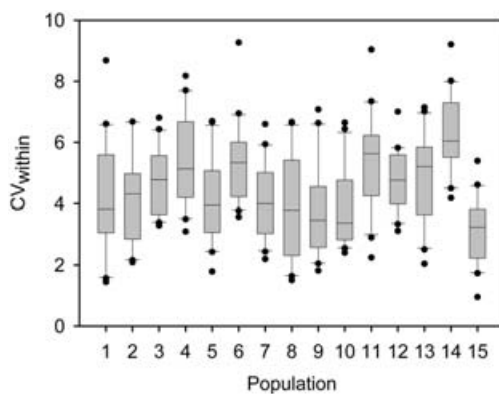


FIG. 7.2 Variation across 15 southeastern Spanish populations of the shrub *Lavandula latifolia* in within-plant variability in corolla length, as estimated with  $CV_{\text{within}}$  (defined in chapter 3). Box plots show the 10%, 25%, 75%, and 90% percentiles of the distributions of plant  $CV_{\text{within}}$ . Plant values beyond the 10–90% range are shown as dots. Populations are significantly heterogeneous with regard to their mean  $CV_{\text{within}}$  values ( $\chi^2 = 75.6$ ,  $P < 0.001$ , Kruskal-Wallis ANOVA). Twenty plants were sampled per population, with 20–25 flowers measured per plant (additional information on these *L. latifolia* populations may be found in Herrera 2004; Herrera, Castellanos, and Medrano 2006).

and Medrano (2006) demonstrated significant geographical differentiation in corolla length on the basis of conventional analyses based on plant means alone. The data plotted in figure 7.2 show, in addition to population differences in plant means, significant differences in levels of within-plant variability in corolla length, with each population tending to have its characteristic level of within-plant variation. Some populations are characterized by highly variable individuals (e.g., population 14), while others are consistently made up of constant plants (e.g., population 15). Acknowledging that populations of the same species may also exhibit geographical differences in levels of within-individual variation is a first step toward understanding yet another facet of intraspecific geographical differentiation. This aspect acquires particular importance in relation to the expanded model of phenotypic selection that is proposed in chapter 10, where variability is explicitly incorporated as another trait potentially subject to selection.