

and *Diplasiolejeunea* (A. Schäfer-Verwimp) are a fine addition to this book with the most recent taxonomic updating of these genera and their species. This excellent treatment, *Hepaticae and Anthocerotae of Brazil* (Gradstein et al. 2003), and *Guide to the Bryophytes of Tropical America* (Gradstein et al. 2001) are fundamental and permanent contributions to the development of bryology in the Neotropics. **Literature Cited**—Gradstein, S. R. 1997. Hepatophyta. Pages 9–15. In J. Boggan, et al. (eds.), Checklist of the Plants of the Guianas

(Guyana, Suriname, French Guiana), 2nd ed. Georgetown, Guyana.—Gradstein, S. R., S. P. Churchill & N. Salazar-Allen. 2001. Guide to the Bryophytes of Tropical America. Memoirs of the New York Botanical Garden 86: 1–577.—Gradstein, S. R. & D. P. de Costa. 2003. The Hepaticae and Anthocerotae of Brazil. Memoirs of the New York Botanical Garden 87: 1–318.—Montfoort, D. & R. Ek. 1990. Vertical distribution and ecology of epiphytic bryophytes and lichens in a lowland rain forest in French Guiana. M.Sc. thesis, Herbarium, Institute of Systematic Botany, Utrecht.

Intra-individual Variation

Reviewed by

A. JONATHAN SHAW

139 Biological Sciences Bldg, Box 90338, Department of Biology, Duke University, Durham North Carolina, 27708 U.S.A.

e-mail: shaw@duke.edu

Herrera, Carlos M. 2009. Multiplicity in Plants. Plant Subindividual Variation and Interactions with Animals. 448 pp., 15 halftones, 23 drawings, 19 tables. The University of Chicago Press, Chicago. ISBN 978-0-226-32793-8 (cloth), 978-0-226-32794-5 (paper). \$110.00 (cloth). Price \$40.00 (paper).



The overall theme of this book is intra-individual variation in morphology, chemistry, and function in plants, and the consequences of that variation for the plants themselves and for the animals that interact with them. I should say at the outset that like most authors who write books about “plants,” Herrera really means angiosperms, or at least seed plants. To his credit, he does recognize that the word “plants” is not actually synonymous with seed plants, and does acknowledge in the first chapter that his treatment pertains to sporophytes and that he does not address the phenomenon in gametophytes (thus demonstrating that he is aware that “real” plants have free-living gametophytes that are ecologically and evolutionarily relevant, and might warrant consideration elsewhere). Nevertheless, that is the only comment in the entire book that reflects a more expansive definition of “plants.” Indeed, the only mention of “bryophytes” in

the book (p. 3) is in the context of remarking that branched sporophytes (absent in bryophytes) was a “decisive evolutionary breakthrough” that enabled “the rapid spread and diversification of land plants.” That is to say, bryophytes represent a “pre-breakthrough” stage of plant evolution.

The book consists of ten chapters that follow a logical progression (these are not verbatim chapter titles): (1) introduction, (2) which traits vary within plants, (3) continuous within-plant variation of reiterated structures, (4) distribution of intra-individual variability in time and space, (5) causes of intra-individual variability, (6) organismal mechanisms of intra-individual variability, (7) intra-individual variability as an individual property, (8) consequences of within-plant variation for interacting animals, (9) fitness consequences of intra-individual variability, (10) evolutionary implications of intra-individual variability.

I read and evaluated this book “with two minds”: one, as a plant systematist focused on how these issues might inform my practice of plant identification and views about plant variation, and two, more strictly in terms of the points the author was trying to make in the book. I generally consider that if a book or paper I read, or a lecture I attend, facilitates at least one new way of thinking about a problem, my time was well spent. This book succeeds in that regard.

Chapters 1–3 are devoted to documenting the existence and patterns of intra-individual variation in plants. (Herrera explicitly excludes from intensive consideration, variation among non-attached ramets of a single genetic clone, or genet.) He notes that many or most estimates of intra-individual variation have been for the purpose of accounting for this level of phenotypic variation in statistical analyses of between-individual (and taxon) patterns. Individual variation has been, in that context, regarded as error variance or “noise,” rather than of biological significance. He notes, repeatedly, that the biological importance of intra-individual variation has been neglected and under-appreciated. Indeed, while I find Herrera’s obvious enthusiasm for the importance of intra-individual variation charming, it does lead to some redundancy and even tediousness in the first seven chapters of the book. For readers interested in pursuing the topic of intra-individual variation further, in the primary literature, tables provided on pages 14–15, 46, 51–54, 57, 59–62, 90–92, 124–125, 175–176, 190–191, 235–236, 256–257, 284 give virtually exhaustive lists of traits, patterns of variation, correlates, taxa studied and references. While I find the general topic of this book interesting, I personally did not need (all of) the 210 pages (Chapters 1–7) of accompanying text in which many of the individual studies are described in detail.

The first chapter discusses which plant characters have been found to vary within individuals — the text is broken down into classes of traits; for example, continuously versus discontinuously varying, floral traits, fruits traits, etc. The second chapter focuses on continuously varying traits, with a section on alternative ways of statistically quantifying that variation. Again, different sections within the chapter focus on leaf traits, fruit traits, seed traits, etc. The next chapter (4) addresses the spatial and temporal

patterns of intra-individual variation, while Chapters 5 and 6 focus on the causes and mechanisms underlying within-individual variation. I was a little disappointed that these last chapters did not substantially address patterns in gene expression within plants, a relatively new field of study that that would have modernized the treatment of topics covered in these chapters. All in all, the first six chapters can be summarized as making the case that intra-individual variation is statistically and biologically substantial in plants. Again, while interesting, there were times when my impatience could be best expressed as: “OK, I get it. Now let’s get on with it.”

As a systematist, I found intellectually useful Herrera’s view, well supported in Chapter 7, that different patterns of intra-individual variation can themselves be characteristic of individuals (i.e., have a genetic basis), and of higher level units such as species. Two individuals or species, for example, sometimes differ not only in mean trait value, but also in patterns or levels of within-plant variation. By analogy to the sorts of traits Herrera discusses for seed plants, one individual of a bryophyte species may produce abundant archegonia more or less evenly distributed across branches of a spreading gametophyte, whereas another might produce them clustered at the branch tips. Is that variation genetically-based? Are there intrinsic or extrinsic environmental factors that underlie such variation? Are there correlates such as differences in growth rates, longevity, or competitive ability, among plants with different patterns of intra-plant variation? Many of us who have focused on systematic problems in particular groups of plants know that these differences in patterns of variation occur. In my own work on *Sphagnum*, I find that some species are more variable in morphology across different parts of a single stem than are others. Sometimes one individual of a species appears to be variable along the vertical extent of a single stem whereas another is not, or is less so. Some species consistently have plants that are individually uniform in color whereas others display marked within-individual variation. A particularly intriguing pattern of within-plant variation in morphology occurs in several species of *Pohlia* that produce two qualitatively different types of gemmae; some stems form one type, some the

other, and some both, and the pattern of within-individual variation has a geographic component. Because of their modular growth patterns, bryophyte gametophytes are natural for studies of intra-individual variation. Although some work has been done documenting such patterns in bryophytes, no information regarding the ecological or fitness consequences is lacking.

The last three chapters in Herrera's book address the ecological and evolutionary significance of within-plant variation in seed plants. This is the most interesting and significant part of the book and indeed, the first seven chapters documenting the existence of such variation really just provide the necessary background. Chapter 8 reviews the effects of intra-individual plant variation on interacting animals, in Chapter 9 he focuses on fitness effects on the plants themselves, and in Chapter 10 he addresses the longer-term evolutionary consequences.

The importance of intra-individual variation lies primarily in plant-animal interactions. Herrera focuses on pollinators and invertebrate herbivores because that is where most of the work has been done, but also reviews different sorts of interactions with a broad array of animals. He makes a solid case for both costs and benefits of within-plant variation to interacting animals, and, importantly, that differences in levels of within-plant variation among

individual plants can promote variance-sensitive behaviors in the animals. These behaviors provide the critical link between within- and between plant variation, and between different levels of natural selection. If individuals within a multi-specific community differ in levels (and/or relevant patterns) of within-plant variation, and these impinge on the behavior of phytophagous animals (for example), variance-sensitive behaviors can in turn affect community structure. Similarly, if conspecific individuals differ in variation patterns, and animals selectively interact with plants on that basis, they can facilitate natural selection among individuals based on their within-plant variation patterns. These various costs and benefits to the plants and to other community members that they interact with can affect the evolution of phenotypic plasticity and norms of reaction, and have significant macroevolutionary consequences.

As is the case for many good books, my impression of Herrera's treatise on intra-individual plant variation evolved during the course of my reading. In retrospect, the first seven chapters could definitely be shortened and tailored to readers like myself that do not wake up in the morning and go to sleep at night thinking about intra-individual variation. Ultimately, though, the book offers a refreshing view of an interesting and under-appreciated level of phenotypic variation.

A Welcome New Monograph of the Sphagnaceae of the Southeastern United States

Reviewed by

G. KAREN GOLINSKI

1409 Franklin Avenue, Nashville, TN, 37206, U.S.A.

e-mail: Karen.Golinski@gmail.com

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