Evolutionary Ecology across Three Trophic Levels

GOLDENRODS, GALLMAKERS, AND NATURAL ENEMIES

WARREN G. ABRAHAMSON AND

ARTHUR E. WEIS

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Foreword

Although, as an ecologist with an interest in plant/insect interactions, I have at my disposal close to half a million species that I can legitimately claim as subjects for study, for the past two decades (effectively the entirety of my professional career to date), I have spent much of my time engaged in the study of only two species. One of these species is a small, physically unremarkable brown moth and the other is perhaps charitably described as a noxious weed. I spend my time so occupied not for want of imagination or lack of other opportunities but because I believe fervently that, just as the quality of a physical structure depends not only on its design but on the integrity of its constituent parts, the quality of conceptual knowledge depends on the integrity of its inputs. Not all ecologists or evolutionary biologists approach their disciplines in this precise manner; practitioners of the comparative approach often emphasize breadth over depth, highlighting the need to gather information on a wide range of systems in order to document robustly and unambiguously general patterns. Without question, both approaches are necessary, but this is not to say that everyone will embrace them with equal enthusiasm. I know that my dogged devotion to a tiny fraction of the world's biodiversity has baffled some of my colleagues. One anonymous reviewer of a grant proposal of mine, in fact, argued that, with 80% of what there is to know about these organisms already worked out, it was hardly worth the marginal return to be gained by investing the remaining 20%.

This book, *Evolutionary Ecology across Three Trophic Levels: Goldenrods, Gallmakers, and Natural Enemies,* by Warren Abrahamson and Arthur Weis, is the perfect rebuttal to such an argument. These two authors have personally invested a quarter-century of effort into the study of a wildflower, a fly, and the fly's small circle of enemies; taking into account the person-years invested by collaborators, students, postdoctoral fellows, and other associates, that quarter-century is multiplied manyfold. What these estimable scientists have for their effort is arguably the most thoroughly characterized three trophic level interaction on the planet, a paradigm system to be used with confidence in defining a conceptual framework for the study of ecological interactions in general. At first blush, *Eurosta,* the fly, and *Solidago,* the host plant, seem less likely candidates for intense scrutiny than my small brown moth and noxious weed, but I envy Abrahamson and Weis, and their fellow travelers, the appealing attributes of their system. The lifestyle of the gallmaking fly makes it exceptionally well suited for quantitative measurement and experimental manipulation; the genetics, physiology, and geographic distribution of the plant permit field, laboratory, and greenhouse study; the system's third trophic level is diverse but manageably so; and the history of the system itself—native to North America and remarkably uncontaminated by human interference—allow for reasonably unambiguous evolutionary interpretations of data.

Years of focused study have produced a wealth of information that is, ironically, staggering in its breadth, encompassing not only ecology and evolution but also systematics, physiology, genetics, molecular and developmental biology, behavior, and a range of other subdisciplines within biology. Synthesized in this volume is more than a century of literature, interpreted, and in most cases inspired by, the conceptual framework of natural selection. August Krogh, a great physiologist of an earlier era, wrote in 1929 that "for a large number of problems there will be some animal of choice, or a few such animals, on which it can be studied most conveniently." This principle is the guiding philosophy behind the use of model organisms that is so characteristic of contemporary cell and molecular biology and so generally eschewed by the majority of ecologists in favor of documenting the diversity generated by natural selection. *Solidago, Eurosta,* and *Eurosta*'s natural enemies may well come to be regarded as a model interaction, as it were, for the fields of ecology and evolutionary biology. Ideally, this book will serve not only as a useful source of information but also as a source of new ideas and insights, and as a shining example of the value of a thorough understanding of the organisms themselves to organismal biologists of any stripe.

May R. Berenbaum,
University of Illinois, Urbana

Preface and Acknowledgments

This book presents the results of two and one-half decades of our empirical work on plant-insect interactions. This book, like our work, centers on the ecology and evolution of the interactions among a host plant, goldenrod (*Solidago*), the parasitic insect that induces a gall on the plant stem, *Eurosta solidaginis* (Diptera: Tephritidae), and a suite of insects and birds that are natural enemies of the gallmakers. Although the specifics of this work are driven by the natural history of clonal plants, gallmakers in general, and this gallmaker in particular, our work addresses the theories and concepts that have guided research on plant-insect interactions over the past twenty-five years, and reaches beyond to address general problems in evolutionary biology. Because goldenrod and its insects are amenable to many types of experimental manipulations, we have employed it as a model system to study the ecology and evolution of specialized enemy-victim interactions. As we take readers through our empirical studies with the *Solidago-Eurosta*-natural enemy system, we hope to impress upon them the many steps involved in the interactive relationships among species. The reproductive success of a gallmaker depends on completion of many actions in sequence. At each step in the process of host finding, ovipositing, gall inducing, feeding, and maturing on goldenrod, host-plant characters can facilitate or thwart the gallmaker and thus impose a complex selective regime on the insect. From the plant's perspective, each gallmaker action is a potential selective pressure on one or more plant characters. It is by examining individual systems that the scope of details that impinges on the evolution of interactions becomes apparent.

Why should we study interactions centered on gall-inducing insects? Plant-herbivore interactions encompass a broad range of natural histories, grading from large migrating ungulates, to polyphagous and swift-moving orthopterans, to oligophagous and awkward Lepidoptera larvae to monophagous and sessile aphid nymphs. Although it is important to understand the ecology and evolution of plant relationships for herbivores at all levels of this scale, the greater number of taxa on the specialized, immobile end suggests that evolution here may be more rapid. Gallmaking insects occupy this end of the spectrum. Their natural histories make them apt subjects to explore issues in the evolutionary ecology of plant-insect interactions, and issues on the evolution of species interactions generally. They spend larval development encased in a tumorlike plant growth that they themselves induce. There they receive nutrients and protection from the elements. Conveniently, a gall flags the gallmaker's presence to the investigator and so allows rapid and accurate censusing. Female gallmakers leave a record of their egg-laying activity through oviposition scars they make in the host plant. Furthermore, since the interaction between plant and insect revolves around the induction, growth, and development of the gall, gall appearance can provide information on the success or failure of the inducing insect.

In the past decade an appreciation has grown for the importance of natural enemies as factors that can influence the evolution of plant-herbivore interactions, and the study of gallmakers has led the way in gaining these insights. Most gallmakers support an array of parasitoids and predators. The success or failure of attack by the third trophic level is often determined by features of the gall that control visibility of and access to the gallmaker.

This book addresses a number of major issues including (1) the physiological and demographic consequences of herbivory for host plants, (2) mechanisms of selection against plant susceptibility to attack, (3) the evolution of host-plant choice behavior, (4) the conditions of formation of genetically distinct host races and their potential for subsequent speciation, (5) the value of the extended phenotype concept in evolution of host manipulation, (6) the structure of selection on phenotypic plasticity, (7) the effects of natural-enemy community interactions on the selection regimes for plant-use traits of herbivores, and (8) the evolutionary responses to selection of native species in natural environments.

The scope of this book should interest not only researchers in plant-animal interactions, but also researchers in the more general areas of evolutionary ecology, ecological genetics, physiological ecology, botany, entomology, and parasitology. The depth of detail is sufficient to understand the nature of the questions at hand and the means of arriving at answers, but not so deep as to allow the reader to lose sight of the big picture.

We offer our deep appreciation to our friends, colleagues, and students too numerous to list, who encouraged us to undertake this task. WGA extends his appreciation to James Karr and Madhav Gadgil for posing some of the stimulating questions and ideas back in the early 1970s that initiated this research, and to Otto Solbrig, James Layne, and Chris Abrahamson for their belief in him. He also thanks the many undergraduate and graduate students who have taken his course entitled "Plant-Animal Interactions" at both Bucknell University and Northern Arizona University for their stimulating thoughts and questions. AEW is grateful to Peter Price, Carl Bouton, and Paul Gross for stimulating thoughts about interactions spanning three trophic levels, and to Stewart Berlocher and Michael Lynch for introducing the possibilities in a quantitative genetic approach to evolutionary ecology. We both owe a special debt of deep gratitude to our forerunners who have previously examined goldenrod and its gallmakers. Foremost among these is Lowell D. Uhler, whose doctoral work on this system was an indispensable guide. Several times along the way we made new "discoveries" only to find them concisely laid out in his monograph (Uhler 1951). Our synthesis draws heavily from the unpublished and/or ongoing studies of several of our coworkers. These collaborators include Jonathan Brown, Timothy Craig, John Horner, and Joanne Itami. We greatly appreciate their willingness to freely share their data and insights.

Many postdoctoral fellows, graduate and undergraduate students, and colleagues have contributed appreciably to the collection of the data and the development of ideas contained in this book. Most significant among these are Jonathan Brown, Tim Craig, Wendy Gorman, John Horner, Joanne Itami, Ken McCrea, and Rod Walton. We gratefully acknowledge the efforts of Chris Aadland, Chris Abrahamson, Jill Abrahamson, Warren Abrahamson, Sr., Mark Andersen, Stephen Anderson, Paulette

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Evolutionary Ecology across Three Trophic Levels

CHAPTER ONE

Evolutionary Ecology and the Interactions of Plants with Insects

1.1 AN UNEXPECTED TWIST OF NATURAL HISTORY

For anyone likely to pick up this book, it is unnecessary to document the diversity in the natural histories of the several millions of species inhabiting earth. Yet, almost all students of biology have at some point been jarred to learn of some feature in some organism they did not anticipate from previous experience. However, when such surprises come, even beginning biologists can evaluate their discoveries in a framework that will often lead them to say, "I could have predicted that." That framework is of course evolutionary theory. Dobzhansky's oft-quoted aphorism about the necessity of the evolutionary perspective to make sense of nature (Dobzhansky 1973) may or may not be true. However, it is certain that biologists have successfully employed concepts in evolutionary theory to come up with powerful explanations for both global patterns in the general biota, and for the origin and maintenance of unique traits in single species.

Insects that induce plant galls are one of those unexpected twists of natural history. Gallmakers stimulate their host plant to develop unique, tumorlike growths, galls, that provide them with food and shelter. The relationship is parasitic (Price, Waring, and Fernandes 1987) since the plant receives no benefit in return for the service. Galls are not the masses of undisciplined cells seen in animal cancers or bacterial plant tumors. Rather, gallmakers induce highly specific structures. For instance, several members of the wasp genus *Andricus* (Cynipidae; Hymenoptera) induce galls on *Quercus robur,* the English oak, and on *Q. petraea,* the durmast oak. Both *A. fecundator* and *A. inflator* inject their eggs into buds, but induce rather different galls. The gall of the former resembles a larch cone while that of the latter a peaked globe, about the size of a pea, attended at its base by scales (fig. 1.1). The wasp *Cynipis quercus-folii* induces a globular gall on leaf veins that is referred to as the "cherry gall" because of its size and shape, while *Andricus testaceipes* induces inconspicuous spindle-shaped galls on the same structure. Each of these galls is the result of a specific interaction between the insect and host plant, yet commonalties are apparent. At the center of a gall is a central chamber where the immature stage of the insect develops. It is typically lined with specialized plant tissue, the nutritive tissue, whose cells are rich in cytoplasm (hence rich in protein and other nutrients) and enclosed in thin cell walls (Shorthouse and Rohfritsch 1992). Outer tissue layers are often much tougher, even woody, and protect the gallmaker from the elements and in some cases from its natural enemies. A baroque twist is added to the plant-gallmaker relationship by the animals that are natural enemies to the gallmaker (Askew 1961; Washburn and Cornell 1979; Weis 1982a; Hawkins and Gagne 1989; Cornell 1990; Plakidas and Weis 1994). Most gall inducers are host to a small complex of parasitoid wasps. Most often these wasps use their needlelike ovipositors to drill through the gall tissue, down into the central chamber, where they lay an egg on or in the gallmaker. When the egg hatches, the wasp larva consumes the gallmaker, pupates, and then emerges as an adult ready to repeat the life cycle. Penetrating the gall is a challenge to the wasps, and often successful attack is limited to a "window of vulnerability" (Washburn and Cornell 1979; Craig, Itami, and Price 1990) before the gall grows too thick or too tough. Besides parasitoids, insectivorous birds, usually woodpeckers or chickadees and tits, peck open some galls to extract the gallmakers when other foods are scarce (Tscharntke 1992; Burstein and Wool 1992). Finally, there are those insects, known as inquilines, that oviposit into existing galls and usurp the gallmaker. Their natural history ranges in complexity from beetles that merely eat the existing gall to some wasps (evolved from parasitoids) that induce secondary galls (Hawkins and Goeden 1982). Advancing from the baroque to the rococo, the galls induced by some insects secrete nectar, thereby attracting

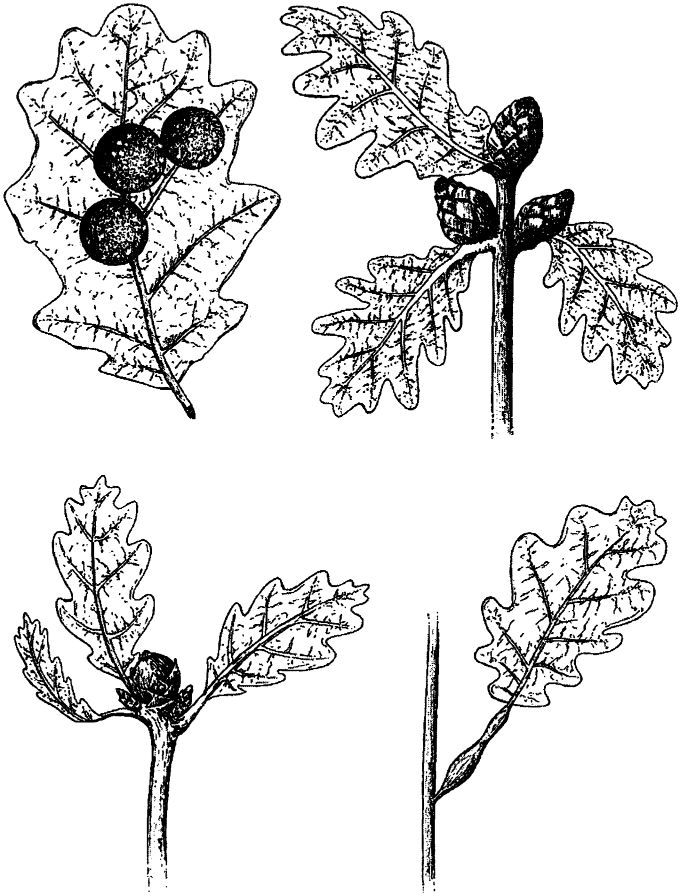

FIGURE 1.1. Four galls induced by cynipid wasps on the English oak, *Quercus robur* (Fagaceae) and the durmast oak, *Q. petraea*. *Top left:* The "cherry gall" induced by *Cynipis quercus-folii* (diameter 2 cm). *Top right:* The "larch-cone gall" induced by *Andricus fecundator* (length 2 cm). *Bottom left:* The globular gall induced by *Andricus inflator* (diameter 0.5 cm). *Bottom right:* The spindle-shaped gall of leaf petioles and midribs induced by *Andricus testceipes*. (Illustration by J. L. Miller)

ants that then deter parasitoids and inquilines (Washburn 1984; Seibert 1993).

Although galls are plant tissue, they can nonetheless be understood as insect adaptations. Natural selection acting on the insect species could favor individuals that upset plant development in ways that improve the nutritional quality or the protective properties of the feeding site. Some have argued that galls first arise as plant defensive structures that contain an otherwise pernicious threat to the vascular system in a nutritious enclosure and thereby obviate any need to bore into vital structures (Cockerell 1890; Hoffman 1985). Although a defensive growth response could provide the initial steps in gall evolution, selection on the gallmaker would easily subvert such a benign response to its own advantage.

This monograph summarizes the beginnings we have made in understanding key features in the evolutionary ecology of a plant-gallmaker-natural enemy interaction. For the past two and one-half decades we have investigated *Eurosta solidaginis* (Diptera: Tephritidae), a fly that induces a spheroid gall on the stem of tall goldenrod (*Solidago altissima;* Compositae). This insect belongs to the family of true fruit flies (i.e., not Drosophilidae), and so is related to the apple maggot, medfly, and other agricultural pests (Wasbauer 1972). The host plant is a common perennial herb of eastern North America. It can be found in old fields, road sides, floodplains, and other places of past disturbance. *Eurosta* is also found on related goldenrods near the edges of its range. A complex of carnivores attack *Eurosta* and its gall. Primary among these are two parasitoid wasps, an inquiline beetle, the downy woodpecker, and, on occasion, the black-capped chickadee. Throughout this book we will refer to the members of this assemblage as the "natural enemies" of *Eurosta.*

At various times we have examined this interaction from the perspectives of the plant, the gallmaker, or the natural enemies, and sometimes from all three. Few such plant-insect interactions have been as extensively investigated, save for some agricultural pests and their crop hosts. However, even after more than 20 years of research, we have made only a beginning. During our studies we have tried to use this system to explore general issues in evolutionary ecology. At the same time, this system has allowed us to investigate issues specific to the evolution of plant-insect interactions, especially those related to evolution of defense, host choice behavior, speciation, and the ecological structure of natural selection exerted by parasitoids and predators on plants and their herbivores.

1.2 PERSPECTIVE ON EVOLUTIONARY ECOLOGY

The evolutionary perspective has led to insights on nature from the level of the molecule to the level of the ecosystem. Foremost among the guiding concepts is that natural selection influences the direction and pace of evolutionary change. Even during times in the history of evolutionary biology when the importance of natural selection's innovative powers (relative to the other causes of evolution) were in doubt, it was still thought to define boundaries for evolutionary change (Provine 1971). The explanatory power of the evolutionary viewpoint, and in particular that of cumulative natural selection (Dawkins 1986), is so great that theory can often run far ahead of experimental confirmation. Theory sets out guidelines for understanding what is possible, or for predicting what is likely. Occasionally an empiricist may be able to decisively test a principle underlying theory. More often, the role of empiricists in evolutionary ecology is to generate the data needed to answer questions on "how strongly" and "how often" theoretical constructs apply to real systems. Chief among our goals has been to understand how selection has operated, or is operating, to shape key features of the goldenrod-gallmaker-natural enemy interaction.

The attempt to understand the ecology of organisms with natural selection dates, of course, to the time of Darwin and Wallace. However, it was with the field studies of David Lack (1947) and the experiments of Kettlewell (1973), and with others of their era (Cain and Provine 1992), that natural selection's power to shape natural history was fully appreciated. As John Endler's book *Natural Selection in the Wild* (1986) showed, selection pressures in natural populations are widespread, and often as strong as those imposed in artificial selection. Adaptive shifts in species following human-made disturbances to the environment (e.g., Antonovics, Bradshaw, and Turner 1971) and in experimental arenas where natural selection was allowed to operate in the laboratory (e.g., Travisano et al. 1995) or in nature (e.g., Reznick and Endler 1982) have shown that selection can lead to very rapid evolutionary results. However, this leaves evolutionary ecology with a problem. If selection pressures are widespread, and potential for response is so great, why don't we see more species evolving on ecological timescales? In view of this problem, George Williams (1992) has warned that to understand natural selection, it may be as important to understand cases in which selection pressure does not cause evolution as to understand cases where it does. This makes the study of constraints an inherent feature in the study of evolutionary ecology.

Evolutionary ecologists working on a particular species can find themselves in the peculiar position of arguing that selection should be changing some character, but cannot due to countervening circumstances. Interactions between enemy and victim species do not result in endless "coevolutionary arms races," and so reasons for observed limits are sought (Thompson 1989, 1994). Finding the limits on selection can be a perilous enterprise since the list of possible constraints on selection is often long, the items on the list not mutually exclusive, and experimental verifications frequently beyond the limits of practicality. This leads to temptation for ad hoc storytelling that may be either adaptive or nonadaptive in flavor, depending on the proclivity of the teller.

Broad-scale, comparative studies may reveal patterns to suggest which constraints are important and which are not. The comparative method has its own problems (Harvey and Pagel 1991; Leroi, Rose, and Lauder 1994), but in the end its precision depends critically on the quality of data on the individual species being compared. In the long run, synthetic, big-picture studies will be what allow us to decide the answers to "how strongly" and "how often" questions on the evolution of enemy-victim interactions. But this can be achieved only through a dialogue between scientists knowledgeable on the natural history of specific systems who are informed by theory and those striving to outline the big picture.

During the time span of our studies, there have been several different phases in the study of plant-herbivore interactions

(Stamp 1992). In some circles the term "coevolution" has gone from buzz word to target of derision. Theories of plant defense have been refined several times (Feeny 1976; Coley, Bryant, and Chapin 1985; Herms and Mattson 1992). Much empirical work has revealed the complexity of insect-host-choice behavior (see Thompson 1988, 1994), and the role of population structure in fine-tuning insect performance (Edmunds and Alstad 1978; Karban 1989). Phylogenetic methods to understand patterns of radiation in herbivore and host (Futuyma and McCafferty 1990; Farrell, Mitter, and Futuyma 1992) were also introduced. Importantly, methods of quantitative genetics have been brought to bear on many questions in evolutionary ecology (see Stearns 1992), and have been particularly fruitful in understanding the structure of selection on plants and their herbivores (Berenbaum, Zangrel, and Nitao 1986; Marquis 1990; Simms 1990; see also Fritz and Simms 1992). In turn, insights into general problems concerning selection have emerged from work on plants and insects (Via 1984, 1991). Some of our work has contributed to these advances. The insights we have gained by studying a single system have given us a unique perspective for comment on others.

1.3 PLANT-INSECT INTERACTIONS AND BASIC QUESTIONS IN EVOLUTIONARY ECOLOGY

The ecological interaction between a plant and its herbivorous insects unfolds as a sequence of events in parallel ontogenies. A young plant is discovered and investigated by a female insect searching for oviposition sites. The female may reject the plant or lay an egg. The larva may eat heavily or may find its food distasteful. After feeding, the plant may regrow lost parts or not, may suffer reduced fecundity, or may complete its life cycle as if untouched. Meanwhile, the insect matures, pupates, mates, and, if female, initiates its own search for oviposition sites. At each event along this ontogenetic path, plant traits can thwart the insect, or at least reduce the impact on plant reproductive success. Conversely, at each step, insect characters determine whether it will be able to overcome barriers presented by the plant and successfully convert plant tissue into fertile eggs, placed in livable habitats. At the same time, the insect characters that determine success on the plant can affect its vulnerability to predator and parasitoid attack. The fundamental expectation for natural selection is that it will adjust the character states in a sequence that tends to increase fitness (see Frank and Slatkin 1992).

The sequential expression of the traits involved in the interaction imposes some important features on the structure of selection. The choice of host plant expressed by an ovipositing female will determine the quality and quantity of resources for her offspring, and so the evolution of the choice behavior depends in part on the subsequent performance of the offspring. In turn, the performance of the offspring evolves in an environment that is determined by parental choice. Similarly, plant infestation levels are determined in part by resistance mechanisms, but the fitness contributions made by a resistance mechanism will depend in part on the plant's ability to tolerate damage. Meanwhile, the selective value of tolerance will diminish as the degree of resistance increases. Because preference and performance, and resistance and tolerance are expressed in sequence, they have an epigenetic interaction concerning fitness (Atchley, Xu, and Vogl 1994). That is, the early expressed trait determines the environment in which the later is expressed, and the later expressed trait defines the selective environment for the earlier. A more formal treatment of the consequences for this type of interaction is presented at the end of the book, but it is a feature that will emerge throughout.

The next chapter presents background information on the *Solidago-Eurosta*-natural enemy interaction. We describe the basic ecology of each species, emphasizing the details that are the stuff of the natural history whose evolution we seek to understand. We acknowledge a debt of gratitude to our forerunners who have previously examined goldenrod and its gallmakers. Foremost among these is Lowell D. Uhler, whose doctoral work on this system was an indispensable guide along the way. Several times along the way we made new "discoveries" only to find them succinctly laid out in his monograph (Uhler 1951).

In the subsequent chapters we present the results of field, greenhouse, and laboratory experiments that have probed the potential for evolutionary change in those plant and insect characters most strongly involved in the interaction, including the potential for host race formation and gallmaker speciation. These chapters revolve around several related questions about the conditions for evolutionary change.

In chapter 3 we ask, What kinds of impacts do gallmakers have on the physiology and growth performance of this clonal host plant? Are the negative effects on growth and reproduction of the type that will result in natural selection on plant defense? On the way to answering these broad questions we describe what is known about *Eurosta*'s gall-inducing stimulus, the effect of gall induction on allocation of biomass, energy, and nutrients in goldenrod ramets, and the integration of these effects across the genet. We reach the tentative conclusion that gallmakers may act as agents of selection when their population levels are very high, or when they attack early in the first few years of the host plant's life.

The plant's perspective is continued in chapter 4, where we ask if individual variation in galling rates are due to genetic causes, and if the influence of genes can be modified by the availability of resources. Our work shows that host plant genotypes vary in their resistance to galling, and that resistance can be expressed at several points in the attack sequence. Some plants are less attractive to ovipositing females while others are less likely to initiate galls once oviposited upon. One of the more intriguing findings is the necrotic response, found to varying degrees in some plant genotypes: cells surrounding newly hatched larvae soon die, resulting in the death of the gallmaker. However, altering nutrient supply can change the relative genotypic differences in resistance. Thus, the potential for resistance evolution can depend not only on the abundance of gallmakers, but on the abiotic background environment as well. In summary, the realized resistance level of an individual host plant will depend on a hierarchy of traits that influence its acceptability and suitability to the gallmaker. Natural populations of goldenrod show ample genotypic variation for these traits to allow a selection response.

In chapter 5 we switch to the gallmaker's perspective. Here we ask to what degree variations in galling rates are the results of choices made by ovipositing females. Plant growth rate and secondary chemistry are used by the fly as cues when selecting among host individuals. However, we find the plant traits which influence *Eurosta*'s preferences do not reliably predict subsequent performance of the offspring. This chapter explores the reasons for weakness of correlation between female oviposition preference and offspring performance.

Gall size is an important factor that determines the strength of the sink that gall formation places on the plant. It is also important from the gallmaker's perspective because parasitoid and bird attack rates on *Eurosta* rise and fall with gall size. Thus both plant and gallmaker have a fitness stake in gall size. In chapter 6 we ask if plants, insects, or both make genetic contributions to variation in gall size. We conclude that although the gall is a piece of plant tissue, it can be considered a part of the gallmaker's extended phenotype. Thus selection acting on the insect can in principle result in evolution of gall size.

The specificity of host-choice behavior in herbivorous insects has long been thought to lend itself to the formation of host-associated races and to sympatric speciation. In chapter 7 we ask if *Eurosta* is divided into host-associated populations. Near the northern edge of *Solidago altissima*'s geographic range, the gallmaker is found on other goldenrods, particularly *S. gigantea.* Genetic differences in phenology and host-choice behavior are seen in flies from the two hosts. Molecular data further confirm some degree of reproductive isolation between both allopatric and sympatric host-associated populations. Our data indicate that some ecological factors, including escape from natural enemies, facilitate host shifting. The environment provided by the novel host plant can cause phenotypic changes in the flies and their galls that facilitate host shifting, such as altered phenology and escape from natural enemies.

The next two chapters examine the selective pressures that parasitoids and insectivorous birds place on the interaction between plant and gallmaker. First, chapter 8 shows that since none of *Eurosta*'s natural enemies are able to curtail the growth and development of the gall, their attack has no beneficial effect on goldenrod. However, gall size is a strong determinant of gallmaker survival. The parasitoid *Eurytoma gigantea* is unable to penetrate large galls, and so imposes a selective pressure on the gallmaker for increased gall size. An opposing selective force is exerted by birds, who preferentially attack large galls. The balance of selection is thus determined by the attack intensity of the two species. Some of the factors that influence attack intensity are examined in chapter 9. We examine the possibility of density- and frequency-dependent selection. This chapter also deals with the partitioning of selective effects between insect genetic variance in gall size and the variance due to the interaction between insect and plant genotype and concludes by asking if an evolutionary response to selection can be seen in *Eurosta.*

The final three chapters deal with evolutionary issues that emerge from our study of goldenrod, its gallmaker, and the natural enemies. A cautionary note is sounded in chapter 10, which shows two examples where environmental effects on growth and development can be mistaken for evolutionary response. Chapter 11 presents a conceptual framework that can bring together ecological and genetic approaches to the evolution of enemy-victim interactions. This framework builds on our view of the defense hierarchy, and the insects response to it. This developmental-genetic view shows how the epigenetic interaction between resistance and tolerance influences their evolution in plants, just as the interaction between insect preference and performance influences evolution of the herbivore feeding niche. We end with a chapter that comments on the relevance of our study of this single system to the evolutionary ecology of plant-insect interactions generally.

CHAPTER TWO

The Stem Gallmaker, Its Natural Enemies, and Goldenrod: A Model System of Tritrophic-Level Interaction

2.1 GALLMAKERS AS A SPECIALIZED HERBIVORE GUILD

Among the many arthropod feeding guilds, one of the most intriguing is that of gallmakers. Gallmakers are unique in that they alter the course of development of plant tissue to form a tumorlike growth from which the insect gains nutrition and protection from the environment (Abrahamson and Weis 1987; Weis and Berenbaum 1989). Gallmakers constitute a functional group broadly scattered across taxonomic lines and include representatives from four kingdoms, two phyla, two arthropod classes, and six orders of insects (Mani 1964; Abrahamson and Weis 1987). Although this feeding habit is found in mites, thrips, moths, weevils, flies, and wasps, it has had its broadest radiation in two families. The Cecidomyiidae (Diptera, gall midges) has more than 5000 gallmakers worldwide (Mani 1964) and the Cynipidae (Hymenoptera, gall wasps) has over 10,000 (Felt 1940). These two families alone account for over 70% of the nearly 1700 insect gallmakers in North America (Weis and Berenbaum 1989).

Many plant species become hosts to gallmakers, but most of the host plant species can be accounted for in relatively few plant families. For example, few gallmakers infest monocots, so that over 90% of the galls worldwide occur on dicots. Among dicots, most galls are found on species within the Rosaceae (rose family), Compositae (aster and sunflower family), and Fagaceae (chestnut and oak family) (Abrahamson and Weis 1987). Generally, gallmakers exhibit a degree of monophagy in host choice and restrict their attack to a single type of plant structure (e.g., bud, leaf midrib, petiole). This and the remarkable degree of specificity of the host plant's reaction to the gallmaker typically result in galls of distinctive morphology where several gallmakers utilize the same host species (Waring and Price 1989; Weis and Berenbaum 1989). Indeed, gallmakers are usually identified by the morphology of their plant gall (Felt 1940).

2.2 GALL PHENOTYPES: CONSEQUENCES OF TWO GENOTYPES

The development of the gall phenotype entails the interplay of two genotypes: that of the gallmaker, which codes for the gall-inducing stimulus, and that of the host plant, which codes for the growth response (Weis and Abrahamson 1986). Dawkins (1982) proposed that a gall structure be considered as an "extended phenotype" of the gallmaker's genome. As such, the ability to stimulate gall formation is an adaptive trait of the gallmaker. Gallmakers secrete substances that function as plant growth and differentiation regulators, overriding the host plant's normal growth systems to produce the gall (Carango et al. 1988; Hori 1992; Raman 1993). Several lines of evidence support this notion including (1) galls typically only develop from meristematic tissue; (2) gall formation involves a change in the pattern by which normally developed tissues are laid down; and (3) gall growth typically depends on the presence of a living gallmaker indicating that a constant supply of stimulant is required (Abrahamson and Weis 1987; Carango et al. 1988). In the subsequent sections, we will offer information about the host plant, gallmaker, and the gallmaker's natural enemies.

2.3 NATURAL HISTORY OF *SOLIDAGO*

Taxonomic Status

The taxonomic status and the phylogeny of the genus *Solidago* (the Latin name makes reference to its healing properties—*solidus* and *ago*—to make whole) are complicated and as yet unresolved (Croat 1972; Melville and Morton 1982; Semple and Ringius 1983; Gleason and Cronquist 1992). Although this native North American genus (except one species—the common Eurasian species *S. virgaurea;* Werner, Bradbury, and Gross 1980) contains well over one hundred species and is among the most ecologically studied wild plants in North America, no comprehensive taxonomic treatment of the genus exists. This is unfortunate given the ubiquitous nature of goldenrod distributions throughout much of North America and elsewhere (as an introduction), and its many interactions with pollinators, herbivores, and their natural enemies.

While goldenrod as a group is easy to recognize, especially during the autumn when their inflorescences dominate in oldfield landscapes, species-level determinations have long been considered difficult because of the number of possible species within a region, the need to use technical characters to separate some taxa, and the occasional occurrence of interspecific hybrids (Semple and Ringius 1983).

Although the base chromosome number for the genus *Solidago* is 9 (*n*), many species are polyploids making multiples of nine common (Beaudry and Chabot 1957; Beaudry 1963; Melville and Morton 1982). For some species, ploidy level and infraspecific classification correlate, but classification of some *Solidago* species is complicated by the existence of more than one ploidy level (e.g., *S. gigantea* that occurs as diploid, tetraploid, and hexaploid taxa; Semple and Ringius 1983).

Solidago Flowering

Goldenrods are insect pollinated and typically self-incompatible (Mulligan and Findlay 1970; Melville and Morton 1982; Gross and Werner 1983). They possess heavy, sticky pollen that is carried by a wide array of invertebrates including honeybees, bumblebees, wasps, syrphid flies, soldier beetles (*Chauliognathus*), moths, and butterflies (Werner, Bradbury, and Gross 1980; Gross and Werner 1983; Semple and Ringius 1983). *Solidago* inflorescences frequently teem with these and other floral visitors during their blooming season even though their tiny florets contain tiny amounts (0.0001 mg sugar per floret; Heinrich 1976) of nectar. Floral visitors are likely encouraged by the high rate at which they can forage proximate florets within and among the numerous heads that compose an individual ramet's inflorescence. Bumblebees, for example, are estimated to handle up to 110 *Solidago* florets per minute (Heinrich 1976).

Goldenrods have frequently been maligned as the cause of late-summer hayfever (Wodehouse 1945). This is unfounded, however, because although the flowering of goldenrods is conspicuous during the late-summer hayfever season, *Solidago* pollen is too heavy to become airborne. Placing the blame for hayfever on goldenrod is a case of a correlation (of hayfever season with showy goldenrod flowers) that lacks cause and effect. Rather, it is ragweed (*Ambrosia* spp.) and other wind-pollinated plant species with their inconspicuous, green flowers, and not *Solidago,* that fill the air with light-weight pollen grains (Lewis and Elvin-Lewis 1977).

The goldenrod species that most often host the goldenrod ball gallmaker are members of the widespread *S. canadensis* sensu lato complex. An examination of the bloom phenologies of three common members of this complex showed that the flowering periods of these species markedly overlap but that they enter bloom in the distinct temporal sequence of *S. canadensis, S. gigantea,* and *S. altissima* (fig. 2.1; Givens 1982; Givens and Abrahamson, unpub. data). The hexaploid *S. altissima* blooms over a longer interval than the other two species, producing a greater niche breadth for *S. altissima* than for *S. gigantea* or *S. canadensis* (fig. 2.1; Table 2.1). Bloom-time overlap is greatest between *S. altissima* and *S. gigantea* in the Canadian data set but between *S. altissima* and *S. canadensis* in the Pennsylvania data set.

Host Plants for E. solidaginis

At least seven taxa of *Solidago* have been reported as hosts of *E. solidaginis,* including *S. altissima, S. gigantea, S. canadensis, S. rugosa, S. (Euthamia) graminifolia, S. serotina* (a synonym of *S. gigantea*), *S. rugosa,* and *S. ulmifolia* (Wasbauer 1972; Novak and Foote 1980; Ming 1989). While such reports provide some indication of the breadth of *Eurosta*'s host preferences, our observations suggest that *E. solidaginis* is more narrowly oligophagous than the literature indicates. The two principal host plants of *E. solidaginis* are *S. altissima* and *S. gigantea;* both are putative

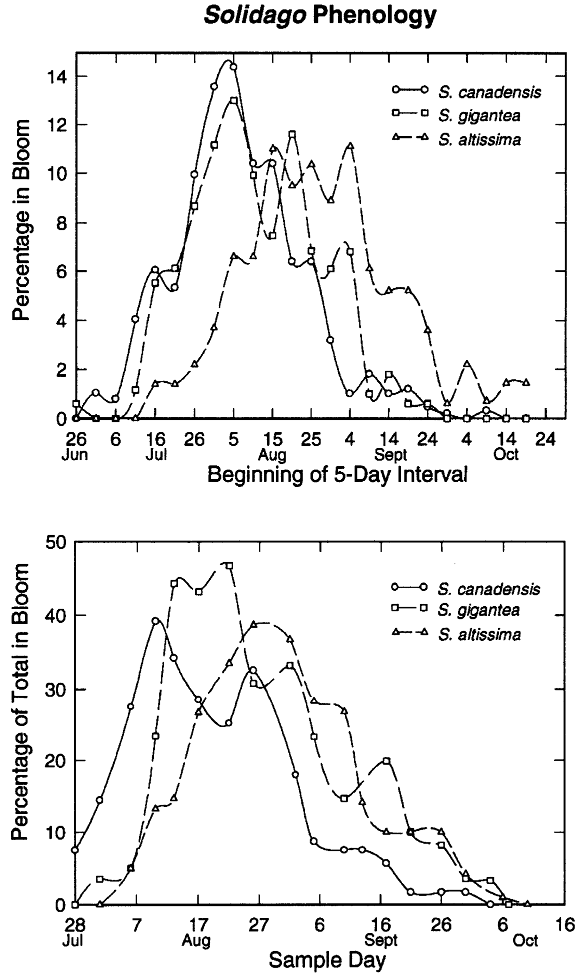

FIGURE 2.1. Bloom phenologies for *S. canadensis*, *S. gigantea*, and *S. altissima* across Canada (*top*) and in central Pennsylvania (*bottom*). Bloom dates for Canadian specimens were tallied from ≈1500 recently annotated specimens of the *S. canadensis* complex in the herbaria of the Ontario National Museum and the Ontario Department of Agriculture in Ottawa, Ontario, Canada. Only specimens in full bloom (or prior to it) were used. Phenology data for central Pennsylvania were recorded for each species along a 5-meter wide, 120-meter long belt transect at the Bucknell University Natural Area approximately every third day following the first appearance of flowers, from 28 July 1981 to 10 October 1981. A ramet was considered in bloom until approximately one-half of all its capitula were open. (Givens 1982; Givens and Abrahamson, unpub. data)

TABLE 2.1. Niche breadth (unweighted) of bloom phenology using Levins's (1968) formula and niche overlap using the formula of proportional similiarity (cf. Schoener 1970).

		Canada Data		Pennsylvania Data	
Niche breadths	*S. canadensis*	0.468		0.079	
	S. gigantea	0.478		0.061	
	S. altissima	0.556		0.093	
		S. can.	*S. gig.*	*S. can.*	*S. gig.*
Niche overlap	*S. gigantea*	0.339	—	0.142	—
	S. altissima	0.558	0.637	0.352	0.015

Source: Data from Canadian herbaria specimens and from ramets censused at the Bucknell University Natural Area (see legend, fig. 2.1; Givens 1982; Givens and Abrahamson, unpub. data).

members of the *S. canadensis* species complex (pers. obs.). In the following paragraphs we offer information about the taxa that have been most commonly reported to serve as hosts for *E. solidaginis.* This information has been summarized from Fernald (1950), Beaudry (1963), Werner, Bradbury, and Gross (1980), Melville and Morton (1982), Semple and Ringius (1983), and is supplemented by our personal observations.

Solidago altissima L. (syn. *S. altissima* var. *scabra),* late goldenrod, is the ancestral and primary host plant of *E. solidaginis* throughout the eastern portions of its range (Abrahamson, McCrea, and Anderson 1989; Waring, Abrahamson, and Howard 1990; Craig et al. 1993; Brown et al. 1995; Brown, Abrahamson, and Way 1996). A strongly clonal species, it frequently forms extensive, nearly pure clusters of ramets. Stems of ramets are covered with a short pubescence but hairs typically become deciduous near the stem's base (fig. 2.2). Leaves are strongly triple-nerved, possessing entire to serrate margins near the apex with a scabrous upper surface and a finely pubescent lower surface (the short leaf pubescence gives plants a gray-green tone). Individual capitula (reproductive heads) contain approximately 10–15 ray florets and 3–7 disk florets. This hexaploid ($2n = 54$) member of the *S. canadensis* complex is common in old fields, roadsides, floodplains, and disturbed sites. Morphologically, *S. altissima* is closest to *S. canadensis* var. *gilvocanescens.*

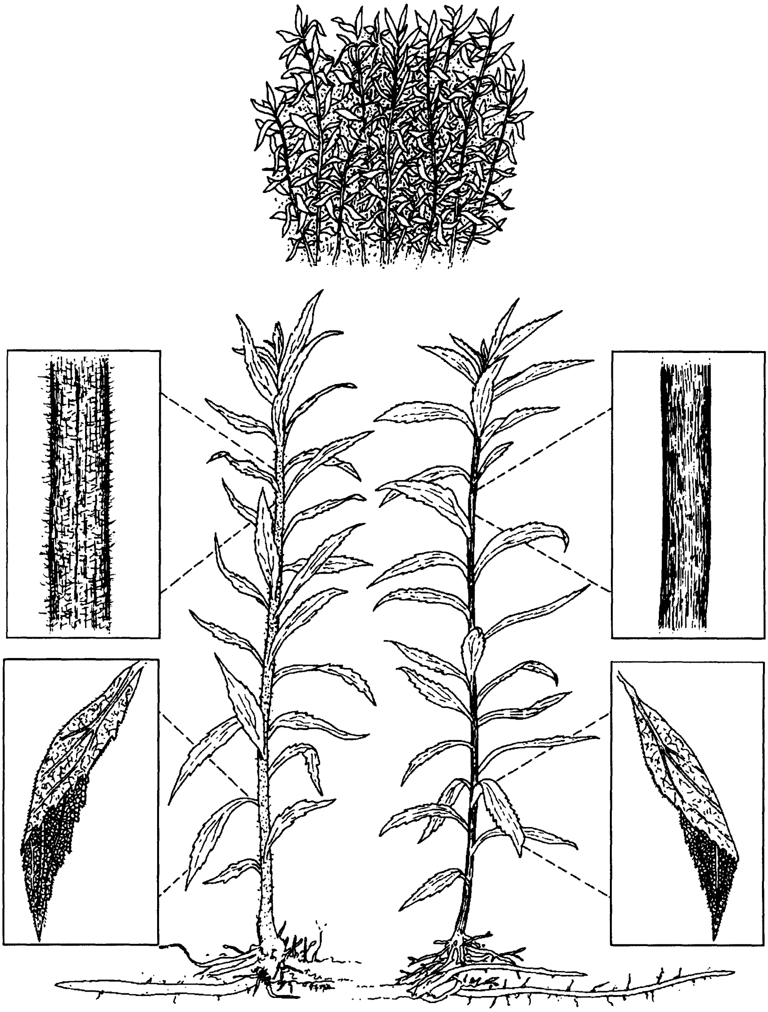

FIGURE 2.2. An old-field goldenrod clone (*top*) shown in midsummer before the onset of flowering. *Solidago altissima* (Compositae) ramet (*left*) with its relatively thick rhizomes. Insets illustrate the scabrous stem and the pubescent leaf underside of *S. altissima* ramets. *Solidago gigantea* ramet (*right*) with its relatively thin rhizomes. Insets illustrate the glaucous stem and leaf underside of *S. gigantea* ramets. (Illustration by J. L. Miller)

Solidago gigantea Ait. (syn. *S. serotina, S. shinnersii*), tall goldenrod, is a common but derived host plant of *E. solidaginis* across northern portions of the gallmaker's distribution (Waring, Abrahamson, and Howard 1990; Craig et al. 1993; Brown et al. 1995; Brown, Abrahamson, and Way 1996). Also a clonal species, its rhizomes are considerably thinner than those of *S. altissima* but like *S. altissima* can create extensive and nearly pure patches of ramets. Stems lack pubescence and are glabrous and glaucous up to the inflorescence. *Solidago gigantea* is the least pubescent member of the *S. canadensis* complex. Leaves are triple-nerved often possessing sharply serrate margins with hairs only on the veins of the leaf underside (fig. 2.2). Individual heads have approximately 7–15 ray florets and 6–12 disk florets. This taxon exists as a diploid ($2n = 18$), a tetraploid ($2n = 36$), and a hexaploid ($2n = 54$, N.B. often occurring as a broad-leaved form) that invades old fields, open woodlands, floodplains, and thickets across its range. The tetraploid taxon appears to be the most widespread. *Solidago gigantea* frequents somewhat more moist sites than *S. altissima* (pers. obs.).

Other species identified as hosts of *E. solidaginis* are less frequent hosts (pers. obs.). *Solidago canadensis* L. (syn. *S. scabra, S. pruinosa*), Canada goldenrod, is an occasional host plant of *E. solidaginis* in northern portions of its range (pers. obs.) and has supported gall formation by *E. solidaginis* in a greenhouse study (Abrahamson, McCrea, and Anderson 1989). Miller (1959) suggested that early reports of *E. solidaginis* galls on this goldenrod may have been due to confusion of *S. canadensis* and *S. altissima.* Another clonal species, *S. canadensis,* has shorter rhizomes than either *S. altissima* or *S. gigantea* and consequently grows with tightly clustered ramets in dense clumps. Stems are glabrous near their bottom but become pubescent from their midpoint to the apex. Leaves are triple-nerved and sharply serrate like those of *S. gigantea.* Leaves have glabrous undersides except for hairs on the major veins. *Solidago rugosa* Mill., rough-stemmed goldenrod; *S. ulmifolia* Muhl., elm-leaved goldenrod; and *S. (Euthamia) graminifolia* (L.) Nutt. (syn. *Chrysocoma graminifolia, S. lanceolata, S. nuttallii),* grass-leaved goldenrod have been reported to be hosts for *E. solidaginis.* We have never observed galls on the latter two taxa and only very infrequently seen them on *S. rugosa.*

CHAPTER 2

Seed Dispersal, Germination, and Performance

The wind-dispersed fruit of *Solidago* is an achene with an attached pappus. Given the small size of these achenes, individual ramets of *Solidago* produce literally tens of thousands of fruits. *Solidago canadensis* and *S. altissima,* for example, have been estimated to produce between 5000 and 19,000 achenes (Bradbury 1973; Hartnett and Abrahamson 1979; Givens 1982). However, the number and quality of achenes can change as a consequence of gallmaker presence (see chapter 4).

Achene mass, pappus length, and fall velocity vary among species (Abrahamson, McCrea, Boomer, and Thum, unpub. data). Achenes of *S. gigantea* are significantly heavier (analysis of variance $F_{2,1227} = 1023, P < 0.001$; 0.13 ± 0.04 mg, ± SD) than those of *S. altissima* (0.08 ± 0.02 mg) or *S. canadensis* (0.05 ± 0.01 mg), and the length of the pappus attached to achenes is longest in *S. gigantea,* intermediate in *S. altissima,* and shortest in *S. canadensis. Solidago altissima* and *S. canadensis* achenes fall significantly more slowly (analysis of variance $F_{2,1227} = 63.7, P < 0.001$; 0.52 ± 0.12 m per sec and 0.52 ± 0.17 m per sec, ± SD, respectively) than the achenes of *S. gigantea* (0.61 ± 0.16 m per sec). Of the three species examined, the achenes of *S. altissima* and *S. canadensis* have the best chances of remaining airborne and being dispersed, while the heavier achenes of *S. gigantea* are likely less dispersible.

We examined the achene germination characteristics of these potential hosts of *E. solidaginis* by simulating April, May, and June night and day temperature regimes for central Pennsylvania in growth chambers (Abrahamson, McCrea, Boomer, and Thum, unpub. data). Temperature has a strong effect on germination rate in all species such that germination began earliest in the June treatment—within 5 or 6 days of placing achenes into the treatment. However, the final rates of germination in May and June temperature regime treatments did not differ. This suggests that the germination of these species most probably occurs during May under natural conditions.

Litter cover and the degree of canopy opening strongly affect seedling emergence, growth, and survival in *Solidago* (Goldberg and Werner 1983). This is not surprising given the colonizing strategies of the old-field *Solidago* species potentially attacked by

E. solidaginis. Unfortunately, relatively few details of *Solidago*'s seedling demography are known but several studies provide insights into the life history and adaptations of the genus.

Greenwald, McCrea, and Abrahamson (1985; unpub. data) explored the seedling performance of closely related *S. altissima* and *S. canadensis* (see Croat 1972) in a greenhouse competition experiment that varied seedling density, moisture level, and ratio of species. DeWit-style replacement diagrams (deWit 1960) suggested that *S. canadensis* had a competitive advantage over *S. altissima* under all experimental conditions, but that soil-moisture level had no significant effect on the outcome of seedling competition between these two species. Extrapolation of these greenhouse findings to natural field conditions where *S. canadensis* and *S. altissima* co-occur imply that *S. canadensis* should dominate and that *S. altissima* should be confined to those patches not exploited by *S. canadensis.* As is frequently the case with extrapolation of simple experimental conditions to the field, the reality throughout much of the range of these two potential *Eurosta* host species is quite different. *Solidago altissima* is often the more common and abundant species. Throughout much of the Mid-Atlantic region and New England, *S. altissima* dominates old fields and roadsides while *S. canadensis* and *S. gigantea* are confined to more mesic ditches or lower patches within old fields and floodplains (pers. obs.). Such field-distribution patterns suggest that there are variables beyond those examined in our greenhouse study that are important to how these species interact in nature. Some of these variables are likely related to climate since *S. canadensis* and *S. gigantea* generally range farther north than *S. altissima* and are normally more abundant in cooler climates (pers. obs.).

We examined the spatial distributions of *S. canadensis, S. gigantea, S. altissima,* and *S. juncea* at the Bucknell University Natural Area along a 5 m wide by 120 m long transect on a gently sloping hillside (Givens 1982; Givens and Abrahamson, unpub. data). The elevated end of the transect had well-drained soil, while soil of the lowest end of the transect was often waterlogged. Soil-moisture samples were collected at 15 m intervals at three dates during a single season.

The four *Solidago* taxa that occurred along the transect were not distributed uniformly. *S. altissima* clones were most dense at the elevated end of the transect, while *S. gigantea* clones predominated toward the lower end. *S. canadensis* clones were restricted to a small region of the lower hillside and *S. juncea* (typically an indicator of dry soils; Werner and Platt 1976) dominated the area of the transect between *S. altissima* and *S. gigantea.* Soil-moisture levels averaged approximately 9% (with relatively high coefficients of variation over the upper half of the transect, 10–22%, because of drying and wetting cycles) at the elevated end of the transect and 17% (with relatively low coefficients of variation over the lower half, 3–10%) at the lowest end. These results suggest that these goldenrods segregate at least in part according to differing tolerances of variance in soil moisture. *S. gigantea* seems to occur primarily on damp to permanently wet ground, while *S. altissima* persists in soils that are (or become) quite dry. Werner and Platt (1976) demonstrated that *S. altissima* (called "*S. canadensis*" in their paper; P. A. Werner, pers. comm.) occupied the largest range of soil moistures of the five species of goldenrod they studied. *S. canadensis* seems to occupy soils with an intermediate range of soil moistures, never on the soggy muck often occupied exclusively by *S. gigantea,* nor on the well-drained sites sometimes occupied by *S. altissima* (Givens 1982).

In a second study, we compared the distributions of goldenrod species by determining the ramet density of each of five species (i.e., *S. altissima, S. gigantea, S. graminifolia, S. juncea, and S. rugosa*) in thirty old fields in central Pennsylvania. Five systematically located soil samples from each field were analyzed for organic matter, phosphorus, potassium, magnesium, calcium, hydrogen, soil pH, and cation exchange capacity (Abrahamson, Ball, and Houseknecht, unpub. data).

Of the five species, *S. altissima* was the most widespread (appearing in twenty-nine of the thirty fields) and the most abundant (densities of 0.2 to 52.9 ramets/m^2). *Solidago gigantea* was the least common (appearing in only twenty of the thirty fields), and *S. juncea* had the lowest densities (ranging from 0.2 to 6.0 ramets/m^2). A detrended correspondence analysis showed that *S. altissima* and *S. gigantea* had the most similar distributions (fig. 2.3). Furthermore, high abundances of these two goldenrods were positively correlated with calcium abundance and less acidic soil. *S. rugosa, S. juncea,* and *S. graminifolia* attained higher

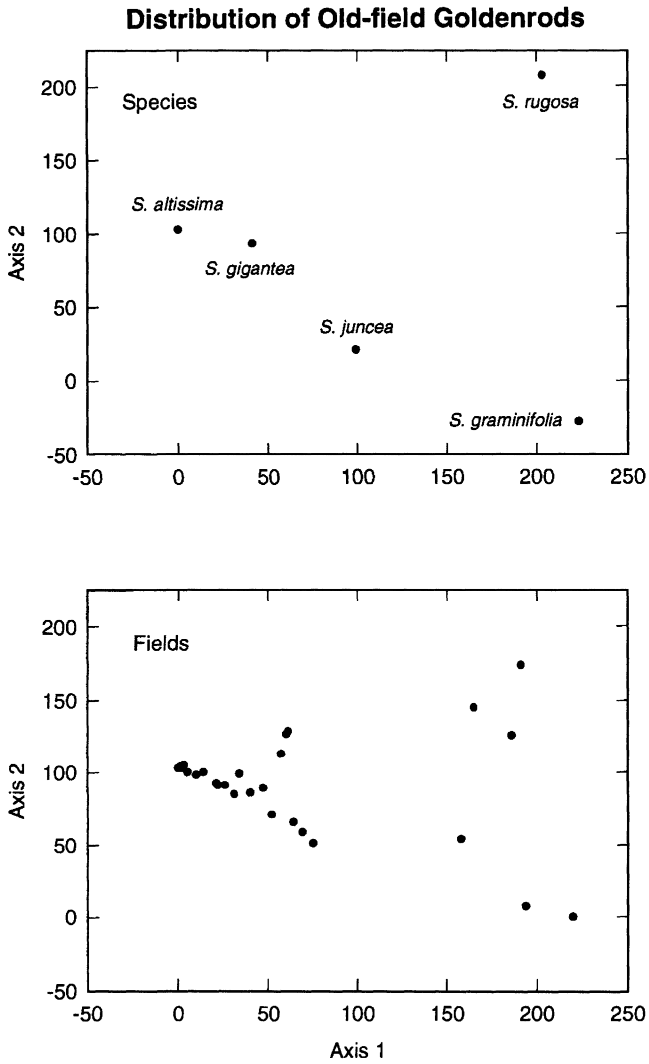

FIGURE 2.3. Species and field ordinations of central Pennsylvania old fields based on 1995 ramet densities of goldenrod species according to a detrended correspondence analysis using PC-Ord (McCune 1993). Each point represents the species position on the first two axes of the ordination. The *x*-axis is correlated with soil pH and calcium abundance such that fields with more calcium and high pH occur nearer the origin. (Abrahamson, Ball, Houseknecht, unpub. data)

densities in fields with more acidic soil. Our finding that *S. altissima* and *S. gigantea* are similar in distribution supports the suggestion of Schmid et al. (1988a,b) that these two goldenrods are ecologically similar.

Clonal Growth Form

The clonal growth of *Solidago* means that clones occur as a clumped resource for ovipositing *Eurosta.* Clonal expansion in the rhizomatous species of *Solidago* occurs by means of rhizome growth outward from the edges of the genotype. The consequence of this growth is a dense cluster of ramets that can grow to several meters in diameter. Clones of up to 10 m in diameter, for instance, have been reported for one *Solidago* taxon in virgin prairie (Werner, Bradbury, and Gross 1980). The clonal habits of the *Solidago* hosts of *E. solidaginis* give host-plant genotypes considerable longevity, albeit at a potential slowing of population-level responses to episodes of selection. Werner, Bradbury, and Gross (1980), for example, reported that clones of *S. canadensis* can persist for more than 100 years.

Schmid et al. (1988a) found that shoot growth and development, leaf size and physiology, and biomass allocation significantly differed among three potential hosts of *E. solidaginis* (i.e., *S. canadensis, S. altissima,* and *S. gigantea*) both in a common garden and in naturally occurring field populations. *Solidago canadensis* had many small and highly productive leaves that enabled rapid plant growth and early flowering followed by the highest resource allocation to seed maturation of the three species. *Solidago altissima* and *S. gigantea* maintained larger leaf areas but they had fewer, larger, less productive leaves and consequently grew slower with delayed flowering relative to *S. canadensis.* Unlike *S. canadensis,* both *S. altissima* and *S. gigantea* continued to strongly invest in vegetative activities (especially the production of long rhizomes) during seed maturation. Schmid et al. (1988a) interpreted these contrasts as differential investment in sexual reproduction, on one hand (*S. canadensis*), versus clonal growth and expansion, on the other (*S. altissima* and *S. gigantea*). As a consequence of these life-history differences, *S. canadensis* forms compact, more strongly integrated clumps in old fields, while *S. altissima* and *S. gigantea* are characterized by larger, more expansive, but less integrated clumps (Schmid et al. 1988a,b; pers. obs.).

The number of new ramets produced by the previous year's "mother" rhizome varies depending on species and resource availability. Data for potential *Eurosta* hosts *S. canadensis* and *S. altissima* indicate that the mean number of new ramets from a mother ramet ranges from two to over eleven (Werner, Bradbury, and Gross 1980). Smith and Palmer (1976) suggested that new rhizomes branch out from the previous year's ramet with somewhat regular patterns of geometry. Most new rhizomes were reported to extend either in the same direction as the mother rhizome or vary approximately 67° to the right or left of the mother's original direction (Smith and Palmer 1976). In contrast, Cain (1990a) found that branching angles, rhizome lengths, and numbers of daughter ramets varied widely among clonal fragments. Importantly, Cain showed that branching angles were independent of both previous branching angles and rhizome lengths and that the modal direction for *S. altissima* clonal growth was 0°. Cain concluded that clonal growth in this species is highly variable and more consistent with stochastic and random-walk models than with deterministic notions of clonal spread.

Seasonal Patterns of Clonal Growth

In a study of the seasonal growth activity and nutrient movement within clones of *S. altissima,* Abrahamson and McCrea (1985) showed that individual rhizomes were dormant over winter but quickly elongated and produced aerial stems the following spring. Nutrient concentrations in below-ground organs remained stable during winter months. However N, P, K, and Mg levels rapidly increased in new rhizomes approximately one month prior to the emergence of ramets from the ground. Although nutrient concentrations generally declined throughout the growing season due to dilution effects as ramets grew, total nutrient content increased due to rather constant uptake from soil reserves from May through September. *Solidago altissima* uses nutrients efficiently via recycling of many mineral elements among organs over time (Hirose 1975; Abrahamson and McCrea 1985). We suspect that many old-field members of this genus are similar to *S. altissima* in their generalized pattern of growth phenology and nutrient-use efficiency, particularly *S. gigantea* due to its ecological similarity to *S. altissima* (Schmid et al. 1988a,b).

Mother ramet size within *S. altissima* clones affected both the size and number of daughter ramets produced (Cain 1990b). Small rhizomes, for instance, tended to develop into small ramets, and smaller ramets had lower survival and fecundity than larger ramets. Given the relationship of ramet size and probability of survival, insect herbivores such as *E. solidaginis* that oviposit early in the growing season might be able to avoid ramets likely to die by ignoring smaller ramets (see chapter 5).

Herbivores of Solidago

Species of *Solidago* are attacked by a wide variety of insect herbivores. The insect fauna of *Solidago* in central New York is undoubtedly the best-studied example due to the many years of careful work by Richard Root and his students. *Solidago*'s herbivore fauna includes more than one hundred species distributed over at least five orders (Messina 1978; Messina and Root 1980). The subset that commonly attacks *Eurosta*'s principal host *S. altissima* (*S. gigantea* is more poorly studied) includes Hemiptera, Homoptera, Coleoptera, Lepidoptera, and Diptera (table 2.2).

2.4 NATURAL HISTORY OF *EUROSTA SOLIDAGINIS*

Taxonomic Treatment

Species in the genus *Eurosta* Loew are stem, rhizome, or crown gallmakers on various species of goldenrods (*Solidago,* Compositae). *Eurosta* may be most closely related to one of two genera, *Aciurina* Curran or *Valentibulla* Foote and Blanc, both gallmakers on Compositae of the western U.S. As many as twelve species of *Eurosta* have been recognized, all from North America. However, taxonomists have varied in the number of *Eurosta* species recognized (synonomies can be found in Foote, Blanc, and Norrbom 1993). Steyskal and Foote (1977) identified nine species based primarily on variations in the size and position of hyaline and gold areas on the dark background of the wing. More

BLE 2.2. Common insect herbivores of *Solidago altissima* by order, family, species, d functional feeding guild. Many other herbivores feed on *S. altissima.*

der	Family	Species	Feeding Guild
miptera	Miridae	*Lygus lineolaris*	flower feeder
		Slaterocoris spp.	foliage feeder
	Tingidae	*Corythuca marmorata*	mesophyll tapper
moptera	Cercopidae	*Philaenus spumarius*	xylem tapper
	Aphididae	*Uroleucon caligatum*	phloem tapper
		Uroleucon nigrotuberculatum	phloem tapper
leoptera	Chrysomelidae	*Exema canadensis*	Leaf chewer
		Microrhopala vittata	leaf miner (larvae), leaf chewer (adults)
		Ophraella conferta	leaf chewer
		Trirhabda virgata	leaf chewer
		Trirhabda borealis	leaf chewer
pidoptera	Gelichiidae	*Dichomeris* spp.	leaf chewer
		Gnorimoschema gallaesolidaginis	stem galler
	Tortricidae	*Epiblema scudderiana*	stem galler
		Epiblema spp.	stem borer
ptera	Cecidomyiidae	*Asteromyia carbonifera*	leaf galler
		Rhopalomyia solidaginis	rosette galler
	Tephritidae	*Eurosta solidaginis*	stem galler
	Agromyzidae	*Ophiomyza* sp.	leaf miner
		Phytomyza sp.	leaf miner

ources: Summarized from Messina 1978; Hartnett and Abrahamson 1979; Messina and oot 1980; Maddox and Root 1987, 1990; Meyer 1993; Meyer and Root 1993; Raman and brahamson 1995.

recently, Ming (1989) prepared a revision of the genus in which she recognized seven species based on morphological and life-history attributes. Ming's (1989) revision is also included in the *Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico* (Foote, Blanc, and Norrbom 1993).

The goldenrod ball gallmaker was placed in the genus *Eurosta* Loew and designated *solidaginis* Fitch by Coquillett (1910). Later, Curran (1923, 1925) described two varieties: *fascipennis,* which he reported to occur on one or more prairie species of goldenrod; and *subfasciatus,* which occurred only on *S. canadensis* (more likely *S. altissima* by today's taxonomic treatments). Ming's (1989) revision of the genus *Eurosta* follows Curran to a degree in suggesting that *E. solidaginis* exists as two subspecies: *E. solidaginis* subsp. *solidaginis* (Fitch) throughout the eastern U.S. and *E. solidaginis* subsp. *fascipennis* Curran in the western U.S. The two subspecies can be distinguished as adults by differences in their wing patterns. The eastern subspecies has three distinctly separated, triangular hyaline areas that are broadly based on the wing margin. However, in the western subspecies, two of these hyaline areas are connected to form a band across the wing (Ming 1989).

Additional differentiation may be occurring within *E. solidaginis*. Both subspecies of *E. solidaginis* described by Ming (1989) are conspicuous gallmakers throughout their ranges; however, Stoltzfus (1989) reported that *E. solidaginis* can attack *S. canadensis* in Iowa without forming a gall. This non-gallmaking *E. solidaginis* occurred infrequently in the Iowa populations examined, with only sixteen adults emerging from some 2335 collected stems (<0.7%). Individuals of the non-gallmaker do not tunnel in the host plant's stem; instead they create a small cavity in the stem pith. Stoltzfus (1989) confirmed that the non-gallmaking and the gallmaking *E. solidaginis* can interbreed. Ovipositions by gallmaking females that were crossed to non-gallmaking males resulted in the initiation of two galls. However, no adults emerged from these galls. The non-gallmaking *E. solidaginis* may have moved into enemy-free space as Stoltzfus (1989) found no evidence of *Eurytoma* parasitoid or bird attack. However, it is possible that the lack of parasitoid attack is a consequence of Stoltzfus's (1989) small sample of non-galling *E. solidaginis*. This non-galling *E. solidaginis* may be rare in any given population, but it appears to be widespread. We have very infrequently encountered individuals of the non-galling *E. solidaginis* in Pennsylvania populations.

More recently our laboratory has shown that Ming's (1989) eastern subspecies of *E. solidaginis* is differentiated into two host races: an ancestral host race that infests *S. altissima,* and a derived host race that attacks *S. gigantea* (Waring, Abrahamson, and Howard 1990; Craig et al. 1993; Brown et al. 1995; Brown, Abrahamson, and Way 1996). It is likely that one of the factors facilitating this host shift is an increase in survivorship on the derived host plant relative to the ancestral host. This increase comes as a consequence of reduced mortality from natural-enemy attack in spite of higher early larval death on the novel host due to poor physiological adaptation (Brown et al. 1995; Brown, Abrahamson, and Way 1996). The evidence for and causes of this host shift are discussed in chapter 7.

The relationship of *E. solidaginis* to other species of *Eurosta* is critical to understanding the roles that host association and host shifts have played in the diversification of this genus. On the basis of morphological synaporphies, Ming's (1989) revision of *Eurosta* suggests that the rhizome-galling species (*E. comma, E. cribrata, E. fenestrata,* and *E. floridensis,* as well as the putative rhizome-galler *E. latifrons*) form a monophyletic group (although her conclusions were tentative because of missing data for some taxa). She considered the rhizome-galling habit derived because species of the presumed sister genus *Aciurina* are stem gallers like *E. solidaginis.* A preliminary phylogeny based on mtDNA variation conflicts with this hypothesis (Brown and Abrahamson, unpub. data). We conclude that *E. cribrata* is more closely related to *E. solidaginis* than to the rhizome-galling species *E. comma* and *E. floridensis* (fig. 2.4). Furthermore, our data suggest that the *E. floridensis* haplotype has emerged from within the *E. comma* clade. Because *E. floridensis* attacks a different *Solidago* species than *E. comma* (which itself varies in host association across its range; attacking at least three species of *Solidago*), we hypothesize that diversification in *Eurosta* has proceeded through host-plant shifts that follow major changes in life-history strategy (Brown and Abrahamson, unpub. data). Although much work remains to be done before we fully understand the roles of host association and host shifts in speciation within the genus *Eurosta,* we do understand the roles of host association and a host shift in host-race formation within *E. solidaginis* (see chapter 7).

Geographic Distribution

Both subspecies of *E. solidaginis* are common in North America. Ming (1989) reported that the eastern subspecies ranges from Maine west to North Dakota, and south only to Virginia and Kansas (or see Foote, Blanc, and Norrbom 1993). Uhler

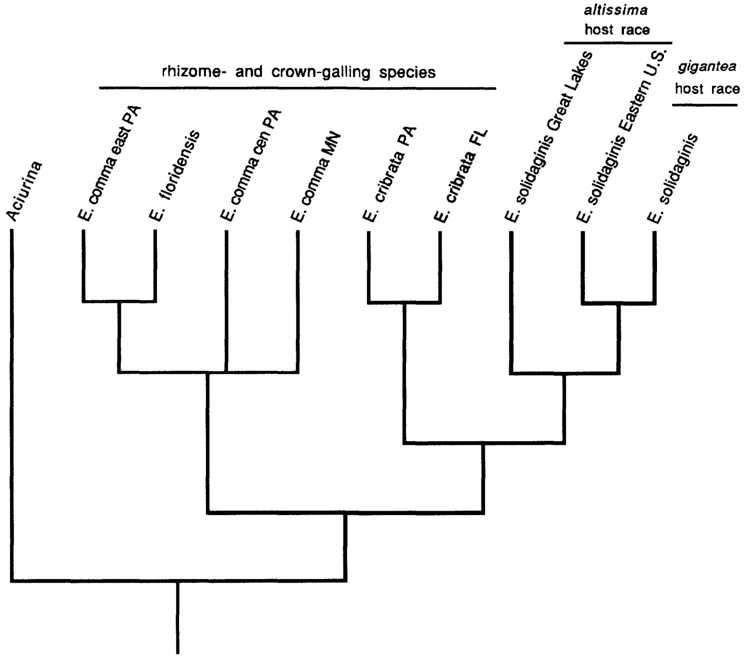

FIGURE 2.4. Preliminary phylogeny of *Eurosta* species based on 492 bp of sequence from mitochondrial cytochrome oxidase I and II genes (consensus of three most parsimonious trees is shown). We used direct sequencing of double-stranded fragments generated by the polymerase chain reaction, and sequences were aligned by eye. A most parsimonious network of relationships among alleles was determined using the EXHAUSTIVE search routine of PAUP3.1.1. Three species (*Eurosta latifrons, E. fenestrata,* and *E. lateralis*) are not included in this analysis. (Brown and Abrahamson, unpub. data)

(1951), however, cited specimens within this region but also specimens of what Ming would recognize as the eastern subspecies from as far south as Texas, Louisiana, and North Carolina. Miller (1959) added to Uhler's (1951) distribution range by confirming *E. solidaginis* populations from Georgia, Kentucky, Michigan, Mississippi, and West Virginia. Our research groups have located populations of the eastern subspecies in sites from New England to Minnesota, including southern Canada and south to northern Florida and Texas (pers. obs.).

Ming (1989) identified the distribution of the western subspe-