

HOST SHIFTS AND SPECIATION IN GALL-FORMING INSECTS

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Abstract. The phylogenetic constraint of gall-forming results in an adaptive syndrome that has emergent properties that determine which modes of speciation are possible. Gall-forming is an adaptive syndrome that entails endophagy and resource manipulation. This adaptive syndrome leads to a high degree of inter- and intra-specific host specialization by the gall-former. Because of this syndrome the herbivore acquires host-plant characteristics that influence its ecological interactions. We consider how this adaptive syndrome influences emergent properties that could influence the probability of speciation in a host shift. The probability of speciation in herbivorous insects depends both upon the probability of a population of herbivores colonizing a new host and upon the probability that the colonists will become reproductively isolated. We conclude that the adaptive syndrome of gall-formers has the following emergent properties that increase the probability of colonization of a new host plant: they may form polymorphisms in response to intraspecific host-plant variation that may preadapt them for host shifts, and they may be subject to frequency-dependent selection so that individuals in a low-density colonizing population may have relatively high fitness. Gall-formers probably lack the ability to shift hosts on a non-genetic basis, such as experience, that would further facilitate host shifts. The adaptive syndrome of gall-formers has several emergent properties that would facilitate rapid reproductive isolation of populations once a host shift was initiated. 1) There is likely to be a negative correlation of performance traits (survival, reproduction and mating success) required to survive on any pair of host plants. 2) Gall-formers have a genetically based host preference, that is not easily altered by experience. 3) Mating occurs on the host plant. 4) Gall-formers are under strong selection to adapt to the phenology of the host plant on which they oviposit. A key determinant of both the probability of a host shift and of subsequent reproductive isolation is the number of genes involved in shifting host preference and the ability to survive on a new host. This has not been determined for any gall-forming species. An examination of the assumptions of sympatric and allopatric models of speciation shows that gall-formers are more likely to speciate sympatrically.

Key words: allopatric speciation, *Eurosta solidaginis*, gall-former, host race, host shift, *Solidago altissima*, *Solidago gigantea*, sympatric speciation.

INTRODUCTION

Gall-formers and Speciation

The basic processes of speciation in herbivorous insects are poorly understood, despite long debate (Bush 1982, Bush and Howard 1986, Tauber and Tauber 1989). The rate at which speciation proceeds, the genetic changes involved in speciation, the ecological conditions promoting speciation, and the degree of geographic separation between populations necessary for speciation are all poorly known. Specifically, the process of speciation in gall-forming insects has not been extensively explored.

In this chapter we review the evidence for how speciation proceeds in gall-forming insects. We believe that the phylogenetic constraints of gall-forming produce an adaptive syndrome with emergent properties that are crucial in determining the avenues by which speciation can occur. Our usage of the terms, phylogenetic constraint, adaptive

syndrome and emergent properties follows that of Price *et al.* 1990). An adaptive syndrome has been defined by Eckardt (1979) as “the coordinated set of characteristics associated with an adaptation or adaptations of overriding importance, e.g. the manner of resource utilization, predator defense etc.” Price *et al.* (1990) defined emergent properties as those insect traits (ecological, genetic, and/or behavioral) that inevitably arise as a result of the adaptive syndrome. This use of emergent properties is commonly used in behavioral discussions and should not be confused with Salt’s (1979) usage: “an emergent property of an ecological unit is one which is wholly unpredictable from observation of the components of the unit”. Our thesis is that the phylogenetic constraints of the gall-former life history strategy leads to an adaptive syndrome that in turn influences the means by which speciation can proceed in gall-formers. We will first discuss speciation models as they apply to herbivorous insects. We will then discuss the pertinent properties of gall-forming insects as they apply to the assumptions of speciation models. Finally, we will review the characteristics of *Eurosta solidaginis*, a stem-galling tephritid fly that forms galls on two *Solidago* species to determine how speciation may be proceeding in this gall-former.

Species Concept

Species concepts are notoriously controversial and it is difficult to find a concept that fits all groups of organisms. We cannot resolve the controversy here. For the gall-formers we are discussing in this chapter, we find it most useful to use the biological species concept of Mayr (1963): “groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups.” We are herein concerned with understanding how a single gene pool can evolve into two gene pools that are recognizably distinct from each other, and this concept is useful in understanding this process.

Models of Speciation

The possible modes of speciation have long been a source of controversy. Mayr (1947, 1963) has maintained that all speciation occurs through processes involving geographic separation of populations and that it is unnecessary and theoretically implausible to invoke models not involving geographic separation. However theoretical studies have indicated that sympatric speciation is feasible under certain conditions (e.g. Bush 1975a,b; Diehl and Bush 1984; Rice 1984). The resulting controversy has centered on the plausibility and the evidence for sympatric speciation. The degree of geographic isolation is just one aspect of the speciation process, and focus on this controversy may have impeded investigation of other important questions about the process of speciation (Bush 1982, Bush and Howard 1986, Futuyma 1987). Both allopatric and sympatric models of speciation make many assumptions about the behavior, genetics and the degree of spatial isolation that are necessary for speciation to occur. Progress towards understanding speciation requires that all of the assumptions of the speciation models be examined. Whether or not the assumptions are true will depend on the adaptive syndrome of the organism.

A common pattern in gall-formers is to find monophagous sibling species or host races on different species of plants (Ananthakrishnan 1984). We will examine in this paper how such patterns could originate. Because of the intimate association of gall-formers and their host plants, any speciation event will involve changes in the relationships with the host plant or plants. We hypothesize two processes could produce new monophagous species: host shift and host losses. In a host shift a population of monophagous gall-formers colonizes a new host plant, speciation could then result if this population becomes reproductively isolated on this new host resulting in two monophagous species: the ancestral and the derived species. In a host loss, a polyphagous species is divided into two populations at least one of which loses the ability to utilize one of the hosts, this is followed by reproductive isolation and the formation of a new monophagous species.

Speciation and Host Shifts

Models have been developed that demonstrate that speciation is feasible during a host shift in herbivorous insects (Maynard Smith 1966; Bush 1975 a, b; Diehl and Bush 1984, 1989; Rice 1984, 1987). Speciation by a herbivore during a host shift requires two processes. First, there must be mechanisms by which a host shift can be initiated. If it is too difficult for a species to colonize a new host plant, then it is unlikely that a population of an incipient species can be established on a new host. Second, once the shift has been initiated then there must be mechanisms by which reproductive isolation can become established between the new and ancestral populations.

When a host shift is initiated a range of outcomes is possible (Fig. 1). The species can become a single polyphagous species, it can split into two species, or it may exist more-or-less indefinitely in two populations that are only partially reproductively isolated which are often termed "host races". The outcome will depend on the balance of forces favoring utilization of both hosts and those favoring reproductive isolation of the two populations. If the balance lies so that there is some degree of reproductive isolation between the populations once a host shift is made, yet the ecological, and or genetic conditions remain such that a "back shift" is possible, two partially reproductively isolated populations may be maintained indefinitely (Fig. 1b). If the two populations are so reproductively isolated once a shift is made that there is little possibility of additional shifts or "back shifts" then either selection and/or drift would proceed fairly rapidly to the formation of two species, and host races would be a transient situation (Fig. 1c).

Finally, there is the situation where reproductive isolating factors once a shift was made are very strong but where the probability of making a shift is so unlikely that it is an unimportant possibility (Fig. 1d). Below we discuss the factors favoring a host shift and those which favor reproductive isolation.

Factors Promoting a Host Shift

The following traits of herbivorous insects may facilitate the acquisition of a new host plant under some conditions:

- 1) Adaptation to one host plant may preadapt an herbivorous insect to utilization of a new host, which could facilitate a host shift. Closely related host plants may differ only slightly with respect to the herbivore's requirements (Bush 1975 a, b). Some insects have the ability to be able to survive on host plants that they do not recognize as hosts (Futuyma *et al.* 1984, Rausher 1984b, Via 1984, Hare and Kennedy 1986, Butlin 1987, Futuyma and Phillipi 1987) indicating that a new host could be acquired by a change in host preference alone. Variation found within the ancestral host-plant species may maintain variation in herbivore emergence times and different adaptations required to utilize a range of host genotypes in a population. Herbivores adapted to utilize extreme host genotypes may be preadapted to utilize extreme genotypes of another closely related plant species. If a mutation arose for a change in host preference, some individuals could survive immediately on the new host.
- 2) If herbivores preferentially oviposit or mate on hosts that they have previously experienced (whether as larvae or adults), the potential for host shifts without the need for genetic changes in preference will be increased (Maynard Smith 1966; Bush 1975 a, b; Futuyma 1983; Diehl and Bush 1989). While the evidence for "larval conditioning" is controversial (Wasserman 1981, Mitter and Futuyma 1983), good evidence exists for adult experience influencing oviposition choice (Prokopy *et al.* 1982, Papaj and Prokopy 1988).
- 3) If few genetic changes are necessary to enable a gall-former to be able to recognize and utilize a new host plant, then a shift would be facilitated. If many mutations are required, then the probability is small that the mutations would be brought together through recombination in a single individual capable of colonizing a new host.
- 4) Frequency-dependent selection can favor the establishment of a herbivore population on a new host. One obstacle to sympatric speciation is the maintenance of mutations for shifts in host preference in the interim preceding further mutations for host utilization (if needed). Individuals ovipositing on a novel host as a result of mutations in genes for host selection will have low fitness until mutations for maximizing performance on the new host arise. Therefore, variants ovipositing on plants other than the optimal host will tend to be eliminated by selection. However, models demonstrate that frequency-dependent selection can preserve variation in habitat selection during colonization of an empty niche, such as a novel host plant, if competition for resources is intense. Initially, poorly adapted morphs can persist because fitness obtained from feeding on an abundant, unexploited host where fecundity is low, can be as high as on the normal host where competition for resources is intense (Rosenzweig 1978; Pimm 1979 a, b; Rausher 1984a; Wilson and Turelli 1986).
- 5) The lower the degree of geographic isolation between host plants, the greater the probability of a gall-former colonizing a new host plant. If a combination of new mutations are necessary for colonizing a new host, the greater the number of colonization attempts there are, the greater the probability that a successful combination will be found.

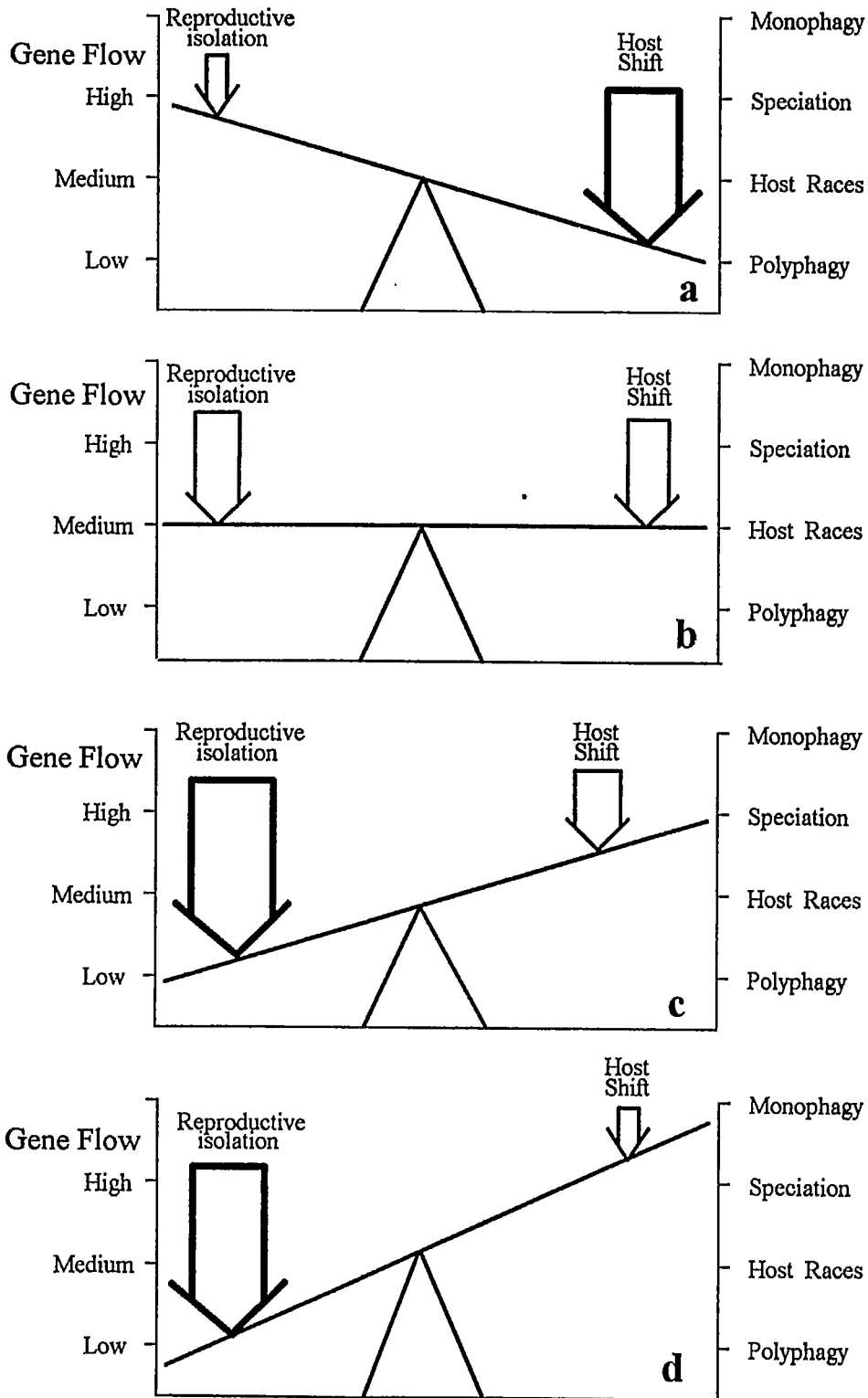


Figure 1.—A representation of how the balance between the forces favoring a host shift and the forces favoring reproductive isolation of populations will determine whether there will be: a) a polyphagous population b) host races c) sympatric speciation d) monophagy.

Factors Favoring Reproductive Isolation

The following factors can promote reproductive isolation in herbivorous insects:

1) Mating on the host plant. The requirements for sympatric speciation can be relaxed if mate choice is coupled with host selection (Bush 1975a, b; Diehl and Bush 1984, 1989; Rice 1984, 1987). This is biologically realistic, since many herbivores mate on their host plant (Price 1980, Diehl and Bush 1984). Assortative mating can arise as a correlated character of host selection (Rice 1984, 1987; Rice and Salt 1988). This coupling removes the selection-recombination antagonism, because the same genes are selected for in both host selection and assortative mating, eliminating the need for linkage between these loci (Rice 1984, 1987; Diehl and Bush 1989). If mate selection is coupled with habitat selection, significant disequilibrium can arise in the alleles for assortative mating/habitat selection and in loci for adaptation (Diehl and Bush 1989). The disequilibrium should be strongest when selection is intense and migration is low. If mating occurs on the host plant then the same genes may be selected for oviposition preference and assortative mating speeding the development of reproductive isolation (Bush 1975a, b; Diehl and Bush 1984, 1989; Rice 1984, 1987).

2) Selection against hybrids. If two host plants require negatively correlated herbivore traits for survival, growth and reproduction on the two plants, then there will be selection against the production of hybrids, leading to selection for premating isolating characteristics (Bush 1975a, b).

3) Genetic basis for host preference. If there is a genetic basis for host preference, with high penetrance then no alteration of host preference can be made by environmental conditions, decreasing the probability for oviposition and/or mating on an alternate host plant, which can lead to gene flow between populations. A mutation would be required to change host preference leading to strong isolation of monophagous herbivores.

4) Host preference and performance requires few gene changes. If few genes are involved in determining the ability to recognize and utilize a host then the establishment of reproductive isolation by a colonizing population is more likely. Models have consistently shown (i.e. Diehl and Bush 1989) that if many loci are involved then recombination can rapidly break-up favorable genetic combinations for recognizing and utilizing a new host plants unless linkage is extremely tight.

5) Differences in adaptation to host-plant phenology could lead to divergence of populations. Reproductive isolation on new hosts can be rapid and selection for adaptations to use a new host plant can be strong if herbivore emergence is dependent on host-plant phenology (Wood 1980, Wood and Guttman 1983, Wood and Keese 1990, Wood *et al.* 1990). Since emergence times of many herbivores are cued to host-plant phenology, oviposition on a new host could shift emergence times, resulting in reproductive isolation. Once the initial reproductive isolation becomes established, intense selection to adapt to the chemistry and nutritional regime of the new host would take place.

6) Geographic isolation. Any degree of geographic isolation will decrease the probability of gene flow during the period when adaptations to a new host plant are being perfected. This will decrease the probability non-assortative mating and the break-up of genetic combinations necessary to utilize a new host plant.

Speciation and Host Loss

Host loss models require that a population of a previously polyphagous species, through selection and/or drift lose the ability to recognize and/or utilize a host, and form a new reproductively isolated monophagous species. Such a process would seem to require a period of geographic isolation of the population, if a species had previously been selected to utilize two species it seems improbable that a new selective force would arise that would lead to the evolution of reproductive isolation in sympatry. Two populations could be separated by a geographical barrier and on each side of the barrier the ability to utilize the alternate host plant would be lost. Each population would become adapted to recognizing and utilizing only the remaining host on its side of the barrier. It is questionable if selection for host adaptation would result in reproductive isolation. If the host plants had been similar enough to have been previously utilized by one herbivore species then it seems unlikely that there would be strongly divergent selection. During a long separation genetic drift could also lead to an accumulation of differences between populations, and could be the more important factor leading to reproductive isolation. Upon being reunited these populations might have become so differentiated that there is reproductive isolation when the populations are reunited.

In contrast to the host shift models, there is no need to identify factors that allow a host shift or colonization of a new host in the host loss models. Establishment and maintenance of reproductive isolation between the populations would be problematic. Why would populations that had been previously been polyphagous not coalesce when they were reunited? The following factors are the same ones identified in the discussion of host shifts that could contribute to reproductive isolation, but the strength of these factors are lost if the herbivore had previously been polyphagous.

1) Mating on the host plant. The populations could have reciprocally lost the ability to recognize the alternate host plant through drift. However, it is difficult to identify selective pressures that would lead to selection not to recognize the alternate host plant. If a population had the ability to discriminate against mating and ovipositing on all but two host plants, then it presumably would not be under further selection to improve its discrimination in the absence of the other host.

2) Selection against hybrids. The two host plants could not have required strongly negatively correlated traits for survival if the species was previously polyphagous. As a result during the period of geographic isolation selection to refine adaptations would not be likely to produce traits that would greatly reduce fitness on the other host plant. There would be little selection to avoid utilizing the other host plant and/or to avoid hybridization upon a subsequent reuniting of the populations.

3) Genetic basis for host preference. It is difficult to identify selective pressures leading to a genetic divergence in host preference: why should a genetic preference for avoiding a plant that isn't present evolve? Presumably an insect that utilized two hosts, had already evolved the ability to differentiate between these plants and all other plants. There would only be selection to avoid the other host plant once the populations were reunited if the plants required different survival traits, which we have argued above is unlikely. Genetic drift could account for differences in host preference given a sufficient time period.

4) Differences in adaptation to host-plant phenology could lead to divergence of populations. Again, it is difficult to identify a reason why populations that had previously been able to utilize both host phenologies would not coalesce when they were reunited.

The Adaptive Syndrome of Gall-formers

The adaptive syndrome of gall-formers will influence the modes of speciation that are possible (Fig. 2). All gall-formers are endophages and resource manipulators. Craig *et al.* (1988) defined resource manipulation as "the active improvement of the herbivore's environment initiated by the herbivore". Gall-formers have the ability to control and manipulate the growth of a plant. The degree to which gallers manipulate growth varies widely from simply inducing continued cell proliferation, to the production of complex structures not normally produced by the plants (Rohfritsch 1992). We hypothesize that resource manipulation and endophagy work together to produce two important characteristics: extreme specialization and the acquisition of plant characteristics by the gall-formers (Fig. 2).

Gall-formers are among the most specialized herbivores: most gall-formers feed on a single host species, they feed on a particular part of the plant, and they have preferences for the most rapidly growing plant parts. Gall-formers from a wide range of insect orders are reported to be highly host specific or monophagous (see references in Ananthakrishnan 1984), based on morphological identification of gall-formers. When host preference tests and/or genetic analysis of populations are actually conducted host specificity is almost always found (Koach and Wool 1977, Berube 1978, Craig *et al.* 1993). It is possible that the few reports of a single gall-former species attacking several plants will be identified as sibling species, or host races with closer examination. The causes of the extreme specialization of gall-formers are not clear. We hypothesize that the extremely intimate interaction of gall-formers and their host plants will select for specialization. We argue that it is very difficult for an insect that completes its life inside a host plant, while manipulating it to provide all the resources it requires, to be a generalist. Every shift to a new host plant will require unique adaptations. Endophagous insects in general are more intimately associated with their host plants than free feeders and as a result will be more specialized. Endophagy imposes selective forces that shape the evolutionary potential of gall-formers (Fig. 2). Most gall-former larvae develop from eggs laid inside host tissue; their fitness is completely dependent on the choice of oviposition site by the female. The larvae cannot move to different plants and must be adapted to the particular species and individual where they are developing. As a result inter- and intra-specific host plant variation has a strong potential to influence larval fitness. Internal feeding means that the interaction with both

**PHYLOGENETIC
CONSTRAINT**

ADAPTIVE SYNDROME

EMERGENT PROPERTIES

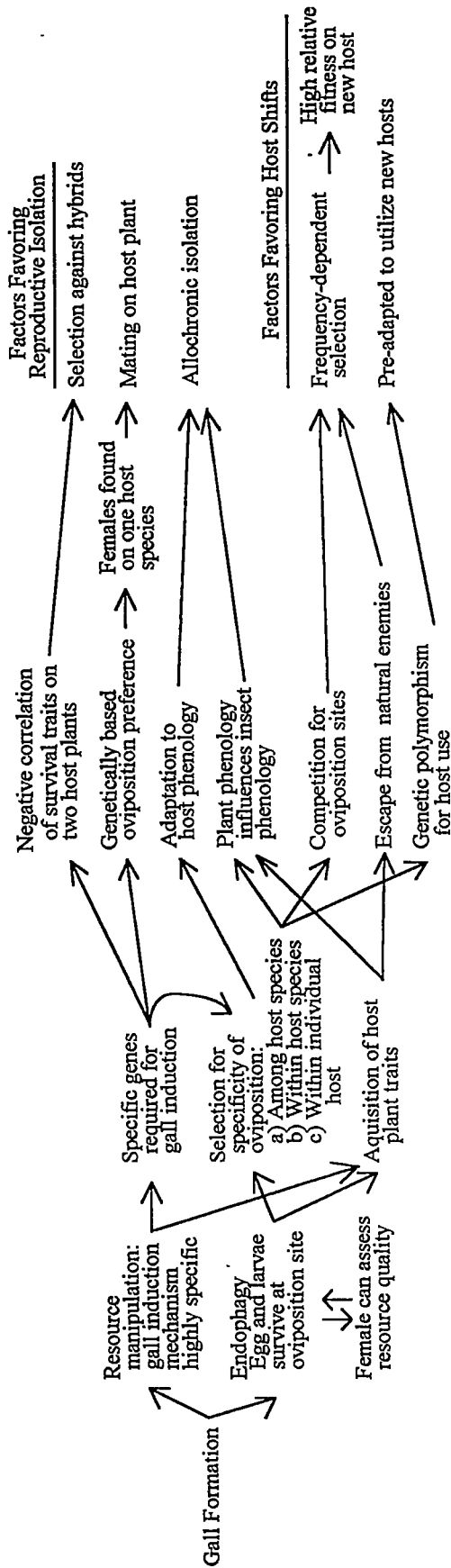


Figure 2.—Phylogenetic constraint, adaptive syndrome, and emergent properties of gall-forming insects that influence the mode of speciation.

the environment and higher trophic levels is mediated by the plant. As a result gall-formers will evolve to be highly responsive to host-plant variation, and the oviposition choices of the female will be highly responsive to host-plant variation.

Resource manipulation, which consists of gall induction for gall-formers, will select for specialization in host use. Gall-formers may utilize a wide range of mechanisms to induce gall growth including behavioral, mechanical, chemical, or genetic manipulation of the host plant to produce gall structures (Hori 1992). The specific manner in which gall growth is induced and maintained is almost completely unknown. Whatever the mechanism of gall induction, there is a strong indication that there must be a match between the genetics of the ability to induce galls by the insect and the susceptibility to gall formation in the plant. As a result, it is hypothesized that an insect species can induce galls only on a single plant species or a very limited number of closely related plant species. If an ovipositing female chooses the wrong plant or site for oviposition, a gall cannot be induced. This will again select for high specificity in oviposition choice (Fig. 2).

Gall-formers are host specific and if host specificity is adaptive, specialization will lead to several emergent properties critical to speciation. First, it should select for inflexible, genetically based, oviposition preferences among species. It is unlikely that individuals can improve their fitness by modifying their oviposition preference among species. Rather, ovipositing on any but the normal host will lead to reduced fitness. Genes for oviposition preference should have high penetrance. If females have fixed host preferences, then males can gain the greatest mating success by searching for them on the host plant. This in turn will lead to mating on the host plant which is a key assumption of speciation models. The high specificity required to utilize hosts could also lead to the development of genetic polymorphisms within a gall-former species. There is often large intraspecific variation in the suitability of host plants within a species for gall formation. This could select for variation within the insect population for utilization of different host plants. This could maintain a pool of genetic variation that might preadapt some individuals of species for utilization of a new host plant. The high specificity for attacking a particular host plant at the time when it has rapidly growing undifferentiated tissue will select for a tight match between insect and plant phenology. Any difference in host phenology will then select for a divergence in emergence times and allochronic isolation among herbivore populations using different hosts.

Implicit in the assumption of selection for high host specificity is the assumption that there is a negative correlation of traits leading to high fitness on two hosts. While this assumption has not been uniformly supported in studies of monophagous herbivores with other adaptive syndromes, the extreme nature of specialization in gall-formers may make this assumption true for gall-formers. If there is a negative correlation between the characteristics that allow survival on two hosts, then hybrids would have low fitness and there would be strong selection for reproductive isolation. High specificity of preference for oviposition sites can also contribute to selection favoring a host shift. Gall-formers prefer rapidly growing plant parts, and these sites are frequently rare, leading to competition for oviposition sites (Price *et al.* 1990). If part of a population shifted to a new host this sub-population could have increased fitness due to escape from competition, even if it suffered decreased fitness from poor adaptation to the host plant.

Acquisition of Host-Plant Characters

A second important feature of a gall-former's adaptive syndrome is the acquisition of host-plant characters. By this we mean that characters of the host plant influence the selective pressures on the gall-former, as well as characteristics of the insect. All endophages acquire some host-plant characters. For example, the susceptibility to natural enemies of all endophages is potentially strongly influenced by the host plant, because natural enemies frequently utilize host plant cues in locating victims (Vinson 1984). Herbivore phenology can be strongly affected by the host plant as demonstrated by the work of Wood and colleagues (Wood 1980, Wood *et al.* 1990), which can be important in establishing reproductive isolation.

Resource manipulators have an even stronger potential for having their evolution influenced by their host plant. A gall is plant tissue and represents an interaction of the insect and plant genotypes with the environment (Weis and Abrahamson 1986). Since the gall is plant tissue, gall characteristics may be influenced by plant characters. The potentials for color, size, shape, and toughness of a gall may be determined by the host plant (Weis and Abrahamson 1986, Craig *et al.* 1990, Craig 1994). These plant characters may determine insect phenology, susceptibility to natural enemies and other characters. A host shift resulting from a single change in a gene for host preference may lead to

changes in all of these characters influencing selection on the insect, without any additional genetic changes. These changes may lead to increased fitness on a new host due to frequency-dependent selection, facilitating a host shift.

Number of Genes Involved in Host Shifts and Host Losses

A key assumption of speciation models for herbivorous insects is the number of genes involved in a host shift. The number of genes in a potential host shift is not determined, as are many of the other characters, by the adaptive syndrome of gall-forming. However, the adaptive syndrome indicates that the number of genes involved in reproductive isolation could be relatively small. Reproductive isolation could result from a change in one or a limited number of genes for host preference, and it would not require a massive reorganization of the genome. The number of genes involved in adapting to a new host shift will depend on the nature of host specificity in gall-formers, and the relatedness of the plant species attacked. To our knowledge, the number of genes involved in a host shift has not been determined for any gall-former.

Speciation and *Eurosta solidaginis*

Eurosta solidaginis is a tephritid fly that induces galls on two species of goldenrod, *Solidago altissima* and *S. gigantea*. We have embarked on a long-term study of the behavioral, ecological and genetic characteristics of *E. solidaginis* to determine how speciation may be proceeding in this gall-former, some of the data is reported in this volume. On the basis of genetic and behavioral evidence we have concluded that the populations are partially reproductively isolated from each other on the basis of host-plant preference, or they are host races by the definition of Diehl and Bush (1984). Our studies, and those of others, allow us to examine whether *E. solidaginis* has the emergent properties of the hypothesized adaptive syndrome of gall-formers. The results are briefly summarized below.

- 1) There is strong selection against hybrids between the host races. Hybrids between the host races have lower survival due to low rates of gall induction following oviposition, and high parasitism rates. Surviving F1's and back crosses are viable and fertile (Craig, Itami, and Horner unpublished data).
- 2) The host races are highly host specific, it is very difficult to induce them to oviposit on the other plant (Craig *et al.* 1993). Studies currently underway indicate that neither adult or larval conditioning influences mating or oviposition site choice (Horner, Itami, and Craig unpublished data). All data to date strongly implicate inflexible genetic control of oviposition- and mating-site choice.
- 3) There is intraspecific oviposition preference. There is a preference for rapidly growing ramets (Anderson *et al.* 1989; Horner and Abrahamson 1992; Craig, Schantz, Itami, and Abrahamson unpublished data).
- 4) A high proportion of mating takes place on the host species from which the fly emerges, leading to a very low rate of mating between the host races (Craig *et al.* 1993).
- 5) The Gigantea fly host race emerges a mean of 4-12 days earlier than the Altissima fly host race, this is enough of a difference to create partial allochronic isolation between host races (Itami *et al.* unpublished data). Results reported in this volume by Abrahamson *et al.* do not support the hypothesis that a character acquired from the host plant (gall color) alters insect phenology.
- 6) There is strong larval competition. Studies of the fly population on *S. altissima* show that there is no avoidance of buds that have been previously attacked (Craig, Schantz, Itami, and Abrahamson unpublished data) and there is strong competition among larvae sharing a gall (Hess 1993). Because buds in the field frequently have a large number of ovipunctures it is possible that there is often intense larval competition. As a result, a shift to a new host could have resulted in frequency-dependent selection leading to relatively high fitness on the new host.
- 7) *Eurosta solidaginis* may have escaped from some of its natural enemies during a host shift (see the discussion by Abrahamson *et al.* in this volume).

8) The genetics of preference and performance are not yet completely understood. We have determined that each host race has a very low survival rate on the host on which it does not normally oviposit (Craig, Itami, and Horner unpublished data), strongly suggesting that genes are required for survival on the two hosts.

Host-race Formation in *Eurosta solidaginis*

It is impossible to definitively reconstruct the past history of speciation or host-race formation. However, we can draw inferences from phylogenetic reconstruction, and we can examine characteristics of currently existing populations to determine which speciation models they fit best. We believe the data supports a model where speciation involves a host shift, is rapid, requires few genetic changes, and does not require a period of geographical isolation.

Models have shown that a period of geographic isolation is not required for host-race formation and/or speciation. Sympatric speciation has been shown to be theoretically possible under a restricted set of conditions. Building on the models of Levene (1953), Maynard Smith (1966) showed that a stable polymorphism at a single locus for habitat selection (e.g. preference) could evolve if (1) density-dependent population regulation operates separately in the two habitats and (2) the selection is strong. However, when assortative mating and habitat preference are controlled by different loci, their mutual inheritance would have to be ensured by linkage in order for sympatric speciation to be possible. This linkage can be broken up faster by recombination than it is built up by selection unless selection is very strong and/or migration is very low. This requirement for tight linkage of a number of loci is a stringent condition for producing sympatric speciation and has been used to argue that sympatric speciation is unlikely (Futuyma and Peterson 1985, Futuyma 1986). However, the requirements for sympatric speciation can be relaxed if mate choice is coupled with host selection, (Bush 1975; Diehl and Bush 1984, 1989; Rice 1984, 1987). This coupling removes the selection-recombination antagonism, because the same genes are selected for both host selection and assortative mating, eliminating the need for linkage between these loci (Rice 1984, 1987; Diehl and Bush 1989). If mate selection is coupled with habitat selection, significant disequilibrium can arise in the alleles for assortative mating/habitat selection and in loci for host adaptation (Diehl and Bush 1989). This disequilibrium should be strongest when selection is intense and migration is low (Diehl and Bush 1989).

Our research to date indicates that characteristics of *E. solidaginis* host races meet the assumptions of these models. First, there is assortative mating primarily due to host plant preference. Second, we have found very low rates of migration: it is very rare for individuals from one host race to mate and/or oviposit on the alternate host plant. Third, selection against ovipositing on the wrong host plant is intense since survivorship is extremely low when flies oviposit on the alternate host. There is also strong selection against mating on the wrong host plant since hybrids between host races have very low viability. All of these characteristics are emergent properties resulting from the adaptive syndrome of gall-forming. This combination of characteristics makes geographic isolation unnecessary for speciation to occur, although it is not incompatible with the data.

Few genetic changes appear to be required for speciation in gall-formers. Only those genetic changes related to host use would need to be altered for speciation to take place, there would be no need for any other characteristics to change. The requirement for only a few genetic changes coupled with the strong selection operating on host choice means that speciation could be very rapid in gall-formers. The divergence of these populations through host loss seems a less parsimonious explanation but it cannot be ruled out. First, as discussed previously, if the species had been polyphagous then there would be forces leading to the re-coalescence of the species. We have discussed above reasons why it would be difficult to prevent populations of a previously polyphagous species from being reunified once the geographic barrier had been removed, unless there had been a long period of separation. Requiring a long period of isolation is an additional assumption not needed for a host shift model. It would also require a specific pattern of distribution of host plants which is also not required in the host shift models. If the polyphagous ancestor had survived in even part of the range it would be a powerful force for gene flow that would cause the reunification of populations. While there are currently areas where one or other of the host races or host plants are lacking (How *et al.* 1993), the current broad overlap of the host plants makes the assumption that the distributions of host plants were once totally isolated questionable. A long period of allopatric isolation with the accumulation of many differences is not indicated by characteristics of the fly populations. Finally, it would require a polyphagous galling ancestor, such polyphagous gall-formers are rare and presumably were rare in the past.

CONCLUSION

We conclude that the adaptive syndrome of gall-formers produce emergent properties that facilitate speciation during a host shift. We have explored the adaptive syndrome of *Eurosta solidaginis* and concluded that it has emergent properties that would facilitate host-race formation and speciation as the result of a host shift. The most restrictive assumption of sympatric models is that there must be strong selection for intrinsic barriers to gene flow. Strong selection for host specialization is produced by endophagy and resource manipulation. Specialization selects for strong genetically based preferences for mating and ovipositing on a single host plant species. Mating on the host plant provides a mechanism for a strong intrinsic barrier to gene flow. The traits for survival on the two host plants are apparently negatively correlated and produce strong selection against the production of hybrids. While the patterns we observe could arise in allopatry, such an allopatric model would involve additional assumptions not necessary with a sympatric model. A plethora of other gall-formers with the same phylogenetic constraints share the adaptive syndrome we have outlined for *E. solidaginis*, and the adaptive radiation in many gall-formers may have occurred via sympatric speciation.

We realize that we have not fully documented all of the emergent properties of *E. solidaginis* we hypothesize to be important in speciation, but we hope our approach to the study of speciation has heuristic value. Determination of whether sympatric speciation is widespread among gall-formers depends on a detailed analysis of the adaptive syndrome and emergent properties of other gall-formers. However, the pattern seen in *E. solidaginis* is common: adaptive radiations of host races or sibling species on closely related host plants (i.e. Price and Roininen 1993). Clear conclusions about how speciation proceeds in gall-formers cannot be made until we know more about the genetics of preference and performance. This in turn may rely on an understanding of the mechanisms of gall induction. Because of the rich possibilities for manipulative experimentation in gall-former systems, these systems offer excellent model systems in which to study the genetics and ecology of speciation.

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