To the Graduate Council:

I am submitting herewith a thesis written by Amy J. McCaskill entitled, "Host race evolution in the pyralid moth *Dicymolomia julianalis* (Walker) on selected hosts in Tennessee." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Entomology and Plant Pathology.

Jerome F. Grant, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor
and Dean of the Graduate School

HOST RACE EVOLUTION IN THE PYRALID MOTH *DICYMOLOMIA JULIANALIS* (WALKER) ON SELECTED HOSTS IN TENNESSEE

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ABSTRACT

Dicymolomia julianalis (Walker) (Lepidoptera: Pyralidae) has a diverse feeding habitats, which range from herbivore to scavenger to predator. Allozyme analysis of fourteen loci was used to evaluate if populations of *D. julianalis* sampled from cat-tail, musk thistle, and common bagworm are genetically differentiated. Significant heterogeneity in allele frequencies exists at eight of nine loci examined. Analyses of population structure indicate that host is more important than geographic location in explaining the distribution of variation. Estimates of migration indicate that a restriction in gene flow exists among populations of *D. julianalis*. Genetic distances indicate that musk thistle and bagworm populations are more similar to each other than both are to cat-tail populations. The phenogram produced by UPGMA of Modified Rogers genetic distances indicate that two fairly separated groups exist in *D. julianalis*. The first group contains only cat-tail populations and the second musk thistle and common bagworm populations. The phenetic analysis indicates that the musk thistle race was most recently derived from the common bagworm race. Results of allozyme analysis indicate that populations of *D. julianalis* are genetically differentiated on these three hosts. As such, host race formation as the first step in sympatric speciation appears to be important in this species.

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CHAPTER I

INTRODUCTION

Speciation processes are composed of at least two fundamental steps, the first is the divergence of populations, and the second is the evolution of reproductive isolation (Maynard Smith 1966, Bush 1975, Nei *et al.* 1983, and Tauber and Tauber 1989). Reproductive isolation may be attained by premating or postmating mechanisms by the direct or indirect effects of natural selection, sexual selection, genetic drift, mutation, or other changes (Mayr 1963, Bush 1975, Nei *et al.* 1983, and Tauber and Tauber 1989). Premating isolation mechanisms include: 1) season and habitat isolation in which potential mating individuals do not meet, 2) behavioral isolation in which potential mates meet but do not mate, and 3) morphological isolation in which mating occurs without successful transfer of sperm. Postmating isolation mechanisms include: 1) gametic mortality in which sperm transfer occurs but the eggs are not fertilized, 2) zygote mortality in which the egg is formed but the zygote dies, 3) hybrid inviability in which a F1 generation is formed but has reduced viability, and 4) hybrid sterility in which the F1 generation is fully viable but partially or completely sterile (Mayr 1963).

The formation of sexually reproducing species has been explained by three models in which populations are either allopatrically, parapatrically, or sympatrically distributed (Mayr 1963, Maynard Smith 1966, White 1968,

Dobhansky 1970, Bush 1975, Futuyma and Mayer 1980, Nei *et al.* 1983, Barton and Charlesworth 1984, Diehl and Bush 1989, and Tauber and Tauber 1989). In allopatric models of speciation, an extrinsic barrier (i.e., geographic isolation) prevents gene flow among populations. Allopatric speciation is by far the most common mode and is more dependent on random processes than events such as shifts in host or habitat (Futuyma and Mayer 1980, Mayr 1982, Barton and Charlesworth 1984, Carson and Templeton 1984, and Tauber and Tauber 1989). Parapatric speciation occurs when populations are adjacent to one another and the boundaries of each overlap. Populations that experience parapatric divergence are situated at the extreme ends along a continuous cline (i.e., change in frequency of an allele or a character over space). Evolutionary forces act differentially on each population along the cline, and thus, the populations diverge (Endler 1977, Barton and Hewlitt 1981, Lande 1982, Slatkin 1982, West-Eberhard 1983, Littlejohn and Watson 1985, Harrison 1986, and Tauber and Tauber 1989). In sympatric models of speciation, an intrinsic barrier (i.e., adaptation to a new host) prevents gene flow among populations (Maynard Smith 1966, Bush 1975, Diehl and Bush 1989, and Tauber and Tauber 1989).

MODELS OF SYMPATRIC SPECIATION

Sympatric speciation is less common than the other two models of speciation and appears to be limited to certain kinds of animals, especially phytophagous insects, animal parasites, and parasitoids (Bush 1975). Most often, disruptive and frequency- or density- dependent selection on resource use within a

population are evoked to explain sympatric speciation (Mayr 1963, Kondrashov and Mina 1986, Bush 1975, Rausher 1984, Diehl and Bush 1989, and Tauber and Tauber 1989). Sympatric speciation usually involves the evolution of specialization to new or unused resources (i.e., hosts and habitats); however, infraspecific competition and sexual selection also have been postulated to lead to sympatric divergence (Tauber and Tauber 1989).

Most population genetic models of sympatric speciation are based on Levene's (1953) model which investigated the maintenance of polymorphism. Levene found that stable polymorphisms could be maintained at two loci that affected fitness between populations in two sympatric habitats if population sizes were regulated independently between the two habitats. Maynard Smith (1966) proposed a model based on the one developed by Levene (1953). Maynard Smith's (1966) model demonstrated that if stable polymorphisms were accompanied by an assortative mating gene and habitat selection, then populations would evolve independently. The presence of an assortative mating gene would lead to matings between individuals adapted to a particular host or habitat.

Much controversy exists concerning sympatric speciation (Futuyma 1986 and Futuyma and Mayer 1980). Early models of sympatric speciation included the assumption that host/habitat shifts were the result of simple genetic changes (Tauber and Tauber 1989). Futuyma and Peterson (1985) and Jaenike (1986) reported that in most insects studied, shifts in association of host/habitat require substitutions at several loci. If simple genetic changes can lead to host/habitat

shifts then a strong positive genetic correlation between host selection and fitness on that host should exist. Few studies have attempted to demonstrate a positive genetic correlation between host selection and developmental or reproductive success and the results obtained thus far have been inconclusive (Tauber and Tauber 1989).

Another point of controversy is if shifts in hosts/habitats resulted from simple genetic change, then strong linkage between the gene(s) responsible for choice should exist, so that co-adapted gene complexes would not be destroyed as a result of recombination. Diehl and Bush (1989) proposed two ways which could circumvent the selection-recombination problem: 1) habitat preference loci also affect fitness in different habitats (i.e., pleiotropy) and/or 2) genotypes with intermediate preference experience reduced levels of fitness.

In insects especially, an association in host or habitat preference and mating site exists because mating often takes place on the host or after dispersal to the habitat (Bush 1969, Bush 1975, and Tauber and Tauber 1989). Some models (Felsenstein 1981, Hoekstra *et al.* 1985, Futuyma 1986, and Fialkowski 1988) could have been pertinent to understanding sympatric divergence on a host and/or habitat utilization, but failed to account for this association (Tauber and Tauber 1989). However, others have not neglected this association (Bush and Diehl 1982, Rice 1984, Jaenike 1988, and Diehl and Bush 1989).

The model proposed by Rausher (1984) demonstrated that when populations are regulated independently, density dependent selection on habitat

preference could lead to diversification of sympatric populations without extremely prohibitive conditions (i.e., unrealistic levels of selection). Diehl and Bush's (1989) model demonstrated that when mating occurred in a novel environment, divergence of sympatric subpopulations could occur when habitat association was polygenically controlled. Sympatric divergence occurred even when habitat preference and fitness differences between races were weak. Jaenike's (1988) model was based on the idea that early adult experience (e.g., contact with larval food) could lead to polygenic differentiation; by facilitating population growth on an accidental or occasional host, and helping to maintain fidelity to the host during genetic diversification. Rice (1984 and 1987) demonstrated that sympatric speciation could occur when disruptive selection on habitat preference was controlled polygenically. Kondrashov's (1983a, 1983b, and 1986) models demonstrated that allelic substitutions at up to eight loci could lead to sympatric divergence with disruptive selection and assortative mating. These models expanded on earlier models which used simple genetic control and indicate that polygenic control of host/habitat association or preference can lead to sympatric divergence (Tauber and Tauber 1989).

Intraspecific competition for limited resources, which leads to frequency- or density-dependent selection, and its effects on sympatric speciation were first introduced by Rosenzweig (1978) and incorporated into several models (Pimm 1979, Udovic 1980, Seger 1985, Wilson and Turelli 1986, and Ginzburg *et al.* 1988). These models resulted in the expansion of the conditions under which

sympatric speciation is likely to occur. Tauber and Tauber (1989) reported that these models led to the expansion of conditions in which sympatric divergence could occur: 1) environment does not have to be heterogeneous, 2) during early stages in the adoption of a new host or habitat, an individual with a poor phenotype could have a high fitness if the resource is plentiful and under-exploited, and 3) formation of stable polymorphisms involving at least two loci which could be maintained in a heterogeneous environment indefinitely. This last result is especially important because it would allow enough time for the evolution of dominance, linkage, and reproductive isolation (Tauber and Tauber 1989).

HOST RACES

Entomological literature is replete with references to biotypes, host races, strains, ecotypes, and other confusing sub-specific labels. Several authors have attempted to eliminate confusion surrounding these taxonomic sub-specific labels (Diehl and Bush 1984, Futuyma and Peterson 1985, and Pashley 1993). Pashley (1993) presents a flow chart for classifying an unknown case into the appropriate sub-specific label. The appropriate term depends on the degree of reproductive isolation between sympatric populations. When no reproductive isolation exists and populations are mating in a random fashion, the organisms are classified as having genetic polymorphism for food choice. When reproductive isolation is complete, separate sibling species will be formed. The situation becomes more ambiguous when the isolation is incomplete, with two possible outcomes, host

races or hybridizing sibling species. It is often difficult to determine whether a taxa represents a host race or a hybridizing sibling species primarily because ecological studies represent a snap-shot in time and not the whole evolutionary history of an organism. Diehl and Bush (1984) defined a host race as "a population of a species that is partially reproductively isolated from other conspecific populations as a direct consequence of adaptation to a specific host."

The most commonly studied and cited example of host race formation is the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae). *Crataegus* spp. (hawthorn) represents the native host to *R. pomonella*. However, agricultural records indicate that during the last 120 years *R. pomonella* has used an introduced plant, *Malus pumila* Miller (domesticated apple), as a host (Bush 1966 and Bush 1969). Other hosts for this fly include cherries (Bush 1966) and rose (Prokopy and Berlocher 1980). To test hypotheses concerning host race formation in *R. pomonella*, several avenues of experimentation have been undertaken including: genetic differences of allozyme loci (Feder *et al.* 1988 and McPheron *et* al. 1988), differences in oviposition behavior (Prokopy *et al.* 1988), and differences in post-diapause emergence time (McPheron *et al.* 1988 and Smith 1988).

Two studies have addressed genetic differentiation of allozyme loci in *R. pomonella* (Feder *et al.* 1988 and McPheron *et* al. 1988). These data indicate that allele frequencies between populations of *R. pomonella* from hawthorn and those from apple are significantly different. McPheron *et al.* (1988) sampled

microsympatric hawthorn and apple populations of *R. pomonella* in Illinois and found differences at two loci among five pairs of populations. Feder *et al.* (1988) sampled three populations of *R. pomonella* from apple and hawthorn in Michigan and found significant differences at six loci. Although sample sizes in these studies were small, the evidence suggests that host races do exist in this species.

Other than with apple maggot, few studies have addressed genetic differentiation among hosts in natural populations using allozyme loci (Jaenike and Selander 1979, Sluss and Graham 1979, Jaenike and Selander 1980, Tabachnik *et al.* 1980, Menken 1981, Guttman *et al.* 1981, Malavasi and Morgante 1983, Pashley 1986, Sturgeon and Mitton 1986, and Waring *et al.* 1990). Results have ranged from no genetic evidence for host races (Jaenike and Selander 1979, Sluss and Graham 1979, and Malavasi and Morgante 1983), to some differentiation among allele frequencies and thus existence of host races (Sturgeon and Mitton 1986 and Waring *et al.* 1990), to striking differences which lead to the conclusion that the organisms represent reproductively isolated sibling species (Jaenike and Selander 1980, Guttman *et al.* 1981, Menken 1981, and Pashley 1986).

MODEL ORGANISM

Dicymolomia julianalis (Walker) is a member of the family Pyralidae and subfamily Glaphyriinae. Pyralidae is generally considered to be the third largest family of Lepidoptera in North America and contains at least 1,375 species (Borror *et al.* 1989). *D. julianalis* is a small (ca. 7-9mm), mottled moth with off white and

reddish brown coloration (Figure 1) (Munroe 1972 and Landau 1993). Larvae of *D. julianalis* are small with an off white body and a brown head capsule (Figure 2).

Dicymolomia julianalis is widely distributed throughout North America. Nova Scotia and Southern Ontario represent the northern limits to its range, whileFlorida and Brownsville, Texas, are the most southern locations from where it has been reported (Munroe 1972 and Landau 1993). *D. julianalis* also ranges from the east coast (Gahan 1909 and Balduf 1937) to as far west as Kansas (Barrows and Gordh 1974) and Oklahoma (Kaufmann 1985).

Larva of *D. julianalis* has been reported as a diverse feeder. Feeding habits range from predator to herbivore to scavenger (Gahan 1909, Allyson 1981, Kaufmann 1985, and Wagner 1985). Food sources from which *D. julianalis* have been reported include: *Opuntia* spp. (prickly pear cactus) (Munroe 1972 and Wagner 1985) , *Gossypium* spp. (cotton) (Allyson 1981 and Wagner 1985), *Astragalus canadensis* (L.) (milk-vetch) (Munroe 1972, Allyson 1981, and Wagner 1985), *Carduus nutans leiophyllus* (Pefr.) Stoj. & Stef. (musk thistle) (Munroe 1972, Powell *et al.* 1992, and Landau *et al.* 1995), *Cirsium lecontei* (Torrey and Grey) (thistle) (Munroe 1972 and Wagner 1985), *Thyridopteryx ephemeraeformis* (Hawthorn) (common bagworm) (Lepidoptera: Psychidae) (Balduf 1937, Barrows and Gordh 1974, Kaufmann 1985, Wagner 1985, and Landau *et al.* 1995), and *Typha* spp. L. (Cat-tail) (Gahan 1909, Claassen 1921, Balduf 1937, Barrows and Gordh 1974, Allyson 1981, Wagner 1985, and Landau *et al.* 1995).

The life cycle, feeding habits, and biological control potential of *D.*

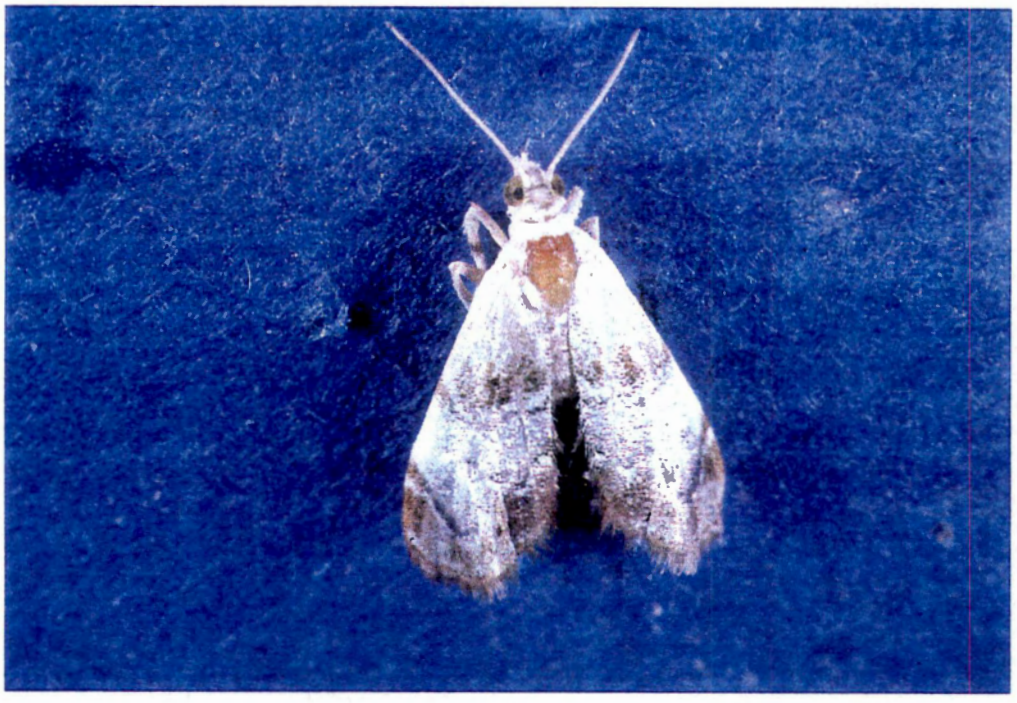


Figure 1. Adult moth of *Dicymolomia julianalis* (Walker).



Figure 2. Larvae of *Dicymolomia julianalis* (Walker) on musk thistle.

julianalis were studied by Landau *et al.* 1995. They suggested that *D. julianalis* had three generations per year on cat-tail, musk thistle, and the common bagworm (overwintering site). Cat-tail was inferred to represent the primary host of *D. julianalis*, since infestation levels were highest on this host (95%). Average levels of infestation of *D. julianalis* collected from musk thistle and bagworm were 12% and 14%, respectively. Their study represents the first attempt to understand the basic ecology and life cycle of this moth.

The broad range of host utilization demonstrated by this species provides an ideal system for addressing questions of host race formation mediated by host specialization. If populations of *D. julianalis* on different hosts are reproductively isolated (i.e., at least partially), then sympatric speciation mediated by host selection may play a prominent role in the life history of this insect. Furthermore, an opportunity exists to examine characteristics of a recent host shift in this species, since musk thistle has only been present in North America for ca. 100 years (Powell *et al.* 1992). Therefore, a two-year study was initiated to further understand the population ecology and genetic background of *D. julianalis*. The specific objectives of this research were to observe genetic variation, population structure, and relative amounts of gene flow within and among populations of *D. julianalis* on cat-tail, musk thistle, and common bagworm using allozyme analysis.

CHAPTER II

MATERIALS AND METHODS

Larvae of *Dicymolomia julianalis* were collected from three hosts, *Typha lattifolia* (cat-tail), *Carduus nutans leiophyllus* (musk thistle), and *Thyridopteryx ephemeraeformis* (common bagworm), from May 1994 through March 1995. Sites for each host were chosen along highways and roadsides in the three major geographic regions (east, middle, and west) of Tennessee. Detailed information on methodology and sampling for each host will be discussed in the following sections.

CAT-TAIL

Populations of *D. julianalis* were sampled at nine sites, with three sites in the eastern, middle, and western regions of the state (Table 1, Figure 3) from 3 May through 17 May 1994. At each site, 15 to 20 flower heads were randomly collected. Flower heads were removed from stems with pruning shears, placed in sealable Ziploc© freezer bags (3.8 liters), and taken to the laboratory for dissection. Cat-tail seed were removed in small portions from the flower head and examined for larvae of *D. julianalis*. Thirty late-instar larvae for all sites were removed from cat-tail flower heads at each site (n=270). Because the egg laying behavior (single or clumped) of *D. julianalis* is not clearly established, no more than two individuals were taken from each flower, to minimize the chance of

Table 1. Locational information for sites from which populations of *Dicymolomia julianalis* (Walker) were collected from cat-tail in Tennessee, 1994.

Region	County	Location	Label*
East	Greene	I-81S, mm 36	2
	Knox	I-40W, mm 376	3
	Washington	I-181N, mm 37	1
Middle	Cumberland	I-40W, mm 327	5
	Marshall	I-65N, mm 32	6
	Putnam	I-40W, mm 290	4
West	Crockett	Hwy-412W, 29.5 miles from Jackson	8
	Henry	Hwy-54N, mm 2	9
	Madison	Hwy-412W, 2.3 miles from Jackson	7

*=Numerical label for all of the populations of *D. julianalis* collected without regard to host (populations will be labeled in this manner throughout text).

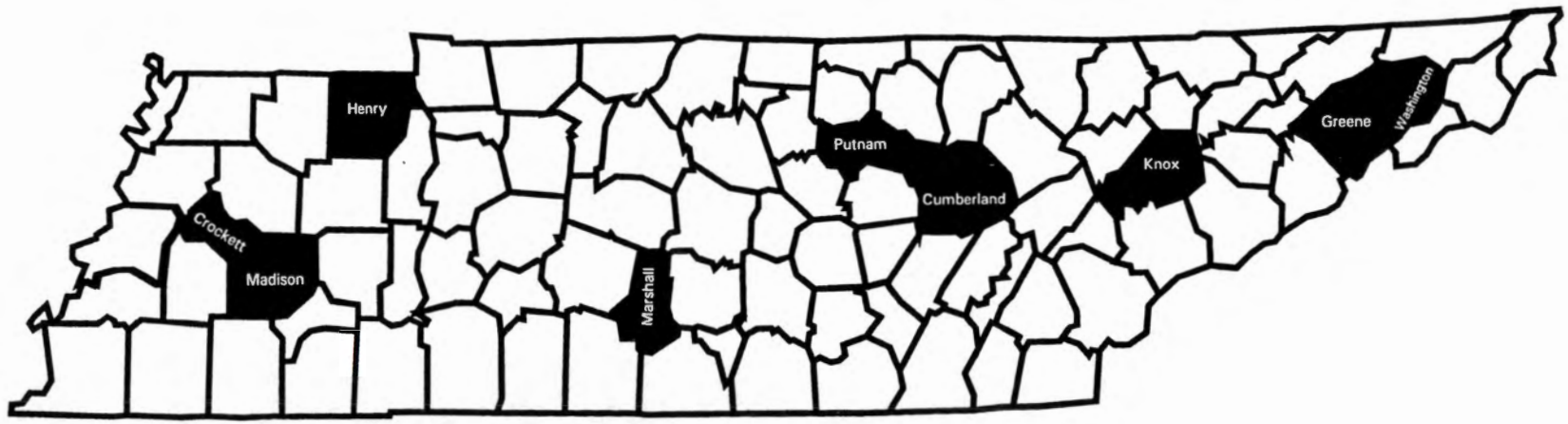


Figure 3. Map showing Tennessee counties from which populations of *Dicymolomia julianalis* (Walker) were collected from cat-tail, 1994.

taking multiple samples from the same set of siblings.

MUSK THISTLE

Populations of *D. julianalis* were sampled from musk thistle at six sites in eastern and middle Tennessee. Because musk thistle is not distributed in western Tennessee, no samples were collected from that area. Three sites in eastern and middle Tennessee (Table 2, Figure 4) were sampled from 26 June through 7 July 1994. Musk thistle sites were chosen in as close proximity to cat-tail sites as possible. At each site approximately 300 flower heads were randomly collected by removing flower heads from the stems. Flowers were then placed into sealable Ziploc© freezer bags (3.8 liters), taken to the laboratory, and dissected. During dissection, the outer thorny sepals were removed, and the remaining flower was examined for larvae of *D. julianalis*. Flower heads were dissected until 30 late-instar larvae were obtained from each site (n=180). A small percentage (<5%) of the musk thistle flowers contained two or three larvae; however, only one larva was used from each flower, to ensure that unrelated individuals were sampled.

COMMON BAGWORMS

Populations of *D. julianalis* were sampled from the common bagworm at nine sites in Tennessee. Three sites were located in eastern, middle, and western Tennessee (Table 3, Figure 5). Bagworms were collected from eastern red cedar, *Juniperus virginiana* L., from 17 February through 12 March 1995. Bags were removed from the tree with pruning shears, placed into sealable Ziploc© freezer

Table 2. Locational information for sites from which populations of *Dicymolomia julianalis* (Walker) were collected from musk thistle in Tennessee, 1994.

Region	County	Location	Label*
East	Greene	I-81S, mm 25	12
	Jefferson	I-40E, mm 428	10
	Knox	I-640N, mm 3	11
Middle	Davidson	I-40E, mm 221	14
	Rutherford	I-24W, mm 70	15
	Wilson	Hwy-231S, 2 miles from I-40	13

*=Numerical label for all of the populations of *D. julianalis* collected without regard to host (populations will be labeled in this manner throughout text).

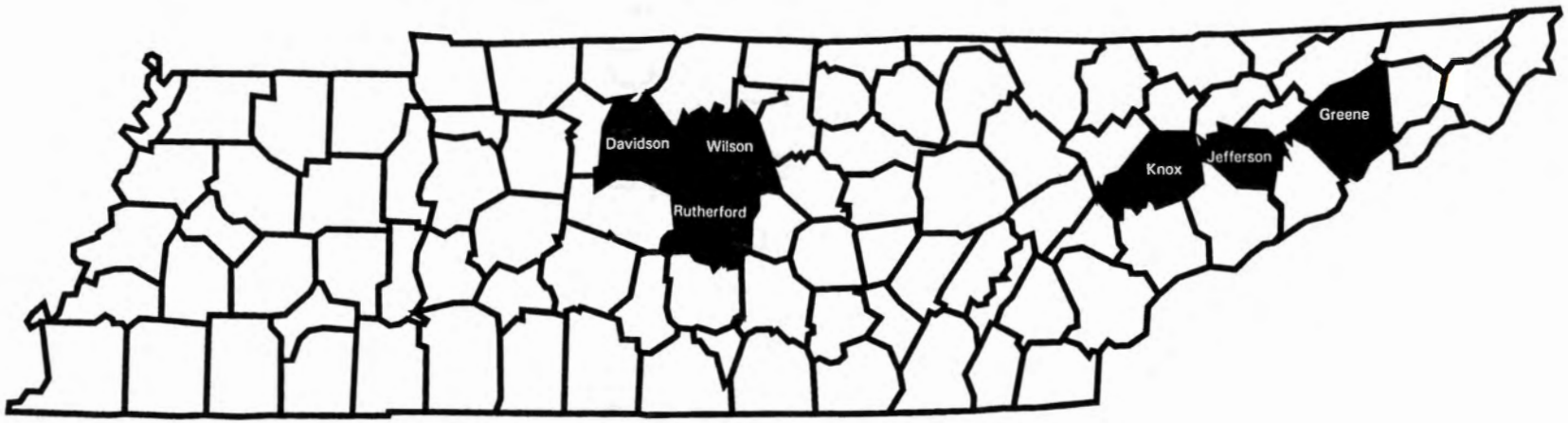


Figure 4. Map showing Tennessee counties from which populations of *Dicymolomia julianalis* (Walker)were collected from musk thistle, 1994.

Table 3. Locational information for sites from which populations of *Dicymolomia julianalis* (Walker) were collected from common bagworm in Tennessee, 1995.

Region	County	Location	Label*
East	Greene	I-81S, mm 25	18
	Jefferson	I-40E, mm 428	16
	Knox	I-40E, mm 398	17
Middle	Davidson	I-40E, mm 232	21
	Smith	I-40W, mm 276	19
	Wilson	I-40W, mm 245	20
West	Madison	I-40W, exit 86 then 22 miles	23
	Crockett	I-40W, mm 56	24
	Haywood	I-40W, mm 83	22

*=Numerical label for all of the populations of *D. julianalis* collected without regard to host (populations will be labeled in this manner throughout text).

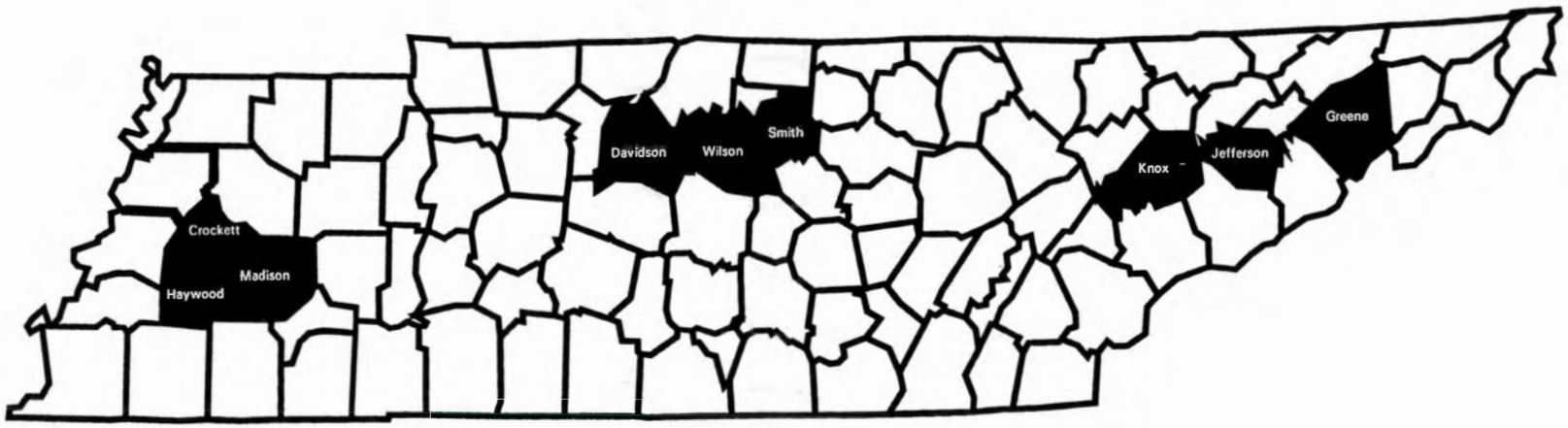


Figure 5. Map showing Tennessee counties from which populations of *Dicymolomia julianalis* (Walker) were collected from the common bagworm, 1995.

bags (3.8 liters), and taken to the laboratory, where each bag was dissected. Larvae of *D. julianalis* were generally located inside the remains of the female bagworm, where they fed upon bagworm eggs. However, some larvae were found within silken tunnels outside the female bagworm, and occasionally *D. julianalis* were found in the bags of eclosed male bagworms. Thirty late-instar larvae of *D. julianlis* were removed from field-collected bags at each site (n=270).

ELECTROPHORESIS

Protein variation was assayed using Type I standard horizontal starch gel electrophoresis (Acquaah 1992). Three buffer systems were used in this study: Tris-Citrate-Histidine pH 7.0 (Tanksley 1979), Morpholine-Citrate pH 6.8 (Clayton and Tretiak 1972), and Lithium-Borate pH 8.1/Tris-Citrate pH 8.5 (Ridgeway *et al.* 1970). Initially, 27 enzyme systems were surveyed; however, only nine were successfully resolved. Recipes for each enzymatic stain were obtained from Acquaah (1992), McDonald (1985), and Pashley (personal comm). Phosphoglucose isomerase (PGI, E.C. 5.1.3.9), Phosphoglucosemutase (PGM, E.C. 2.7.5.1), and α-Glycerophosphate dehydrogenase (GPDH, E.C. 1.1.1.8) were most clearly resolved on discontinuous Tris-Citrate-Histidine pH 7.0 buffer. Hexokinase (HK, E.C. 2.7.1.1), Malic enzyme (ME, E.C. 1.1.1.40), Malate Dehydrogenase (MDH, E.C. 1.1.1.37), and 6-Phosphogluconate Dehydrogenase (6-PGD, E.C. 1.1.1.44) were resolved using the Morpholine-Citrate pH 6.8 which is a continuous buffer system. Flourescent Esterase (EST, E.C. 3.1.1.--), and Glucose-6-phosphate Dehydogenase (G6PDH, E.C. 1.1.1.49) were

electrophoresed using Lithium-Borate pH 8.1/Tris-Citrate pH 8.5 which is a discontinuous buffer system.

All late-instar larvae (n=30) from each site (n=24) were placed into 1.5 ml microcentrifuge tubes directly after removal from host, shock frozen to -196°C in liquid nitrogen, and stored in a freezer maintained at -70° C for approximately one month. Frozen individuals were then ground in 75µl homogenizing buffer composed of 25ml of 0.1M Tris-HCL pH 7.5 containing 10mg of EDTA, 1g of PVP-40T, 25µl of 2-mercaptoethanol, 100µl of tween 20, and 100µl of glycerol. The homogenized solution of each individual was then absorbed onto eight, #3 filter (9mm x 3mm) paper wicks (n=5,760) and stored in -70°C freezer.

Gels were made from hydrolyzed potato starch (Sigma S-4501) and were prepared 24 hrs prior to electrophoresis. Each gel had a volume of 350ml, and 35g of starch was mixed with 75ml of appropriate gel buffer in a vacuum flask, while 275ml of buffer was heated until boiling and then poured into the flask. Forty samples, representing five individuals from eight different populations, were run on each gel. Electrophoresis was conducted at 50 mA until the bromophenol blue dye marker had migrated 8.5-9.0 cm (4-5 hrs) in the anodal direction.

After electrophoresis, each gel was removed from its mold, placed between two pieces of plexiglass and sliced. Spacers (1.5mm wide) were placed on both sides of the gel, and slices were cut with an E(6th) guitar string held by a u-clamp. The number of slices was proportional to the number of enzyme

systems assayed with that particular gel. Each gel slice was placed into a separate staining tray. After mixing ingredients for each enzyme stain, the mixture was poured onto each slice. Each box was then placed into a 37°C oven to incubate until the banding pattern became apparent (approximately 30 minutes-1 hour). The resulting zygograms were drawn immediately after staining. Scoring of genotypes was determined from drawings of gels, with the slowest anodally migrating allele receiving the lowest alphabetic designation. Because *D. julianalis* is diploid organism, single-locus genotypes were composed of two alleles.

DATA ANALYSIS

Data were analyzed using the FORTRAN program BIOSYS-1 (Swofford and Selander 1981). Number of loci, number of alleles, allele frequencies, level of polymorphism, and percent heterozygosity were calculated. Genotypic data for each polymorphic locus at each site were tested for departure from Hardy-Weinberg expectations at each locus using chi-square goodness of fit tests (Sokal and Rohlf 1981) and exact significance probabilities (Haldane 1954). Levels of inbreeding and the distribution of genetic variation among subpopulations were estimated using F-statistics (Wright 1965 and Nei 1977) which can be partitioned into the total reduction in heterozygosity due to nonrandom mating within a subpopulation (F_{IS}) and population subdivison (F_{ST}) components.

Gene flow, or the genetic effective migration rate (Nm), was estimated using the formula $Nm=(1-F_{ST} / 4F_{ST})$ (Slatkin and Barton 1989 and Cockerham

and Weir 1993). To compare migration between populations of *D. julianalis* on different hosts, hierarchical F-statistics were calculated. Patterns of migration between populations from each of the three hosts were analyzed by examining geographical associations in allele frequencies of sympatric host sites [Greene Co. (all three hosts), Knox Co. (all three hosts), Madison Co.(cat-tail and bagworm), Crockett Co. (cat-tail and bagworm), Jefferson Co. (musk thistle and bagworm), Wilson Co. (musk thistle and bagworm), and Davidson Co. (musk thistle and bagworm) by correlation analysis.

Rogers (1972) genetic similarity and Modified Rogers genetic distances (Wright 1978) were calculated to determine the similarity and distances of populations collected from each host. The Modified Rogers genetic distance coefficients were then used to generate a phenogram using the algorithm of unweighted pair-grouping method with arithmetic averaging (Sneath and Sokal 1973).

CHAPTER III

RESULTS AND DISCUSSION

Fourteen loci representing nine enzyme systems in 24 populations of *Dicymolomia julianalis* were assayed. Allele frequencies were calculated for all loci of populations of *D. julianalis* from each of the hosts (Tables 4, 5, and 6). Mean allele frequencies also were calculated for each host from which *D. julianalis* was collected (Table 7). Nine (PGM, PGI, EST-1, EST-2, EST-4, G6PDH, HK-2, MDH-2, and 6PGD) of the 14 loci surveyed were polymorphic (i.e., more than one allele was detected). All other loci (EST-3, GPDH, HK-1, MDH-1, and ME) surveyed were monomorphic (i.e., only one allele).

Heterogeneity of allele frequencies among populations was tested using Pearson chi-square statistic. Significant heterogeneity exists among populations of *D. julianalis* collected from cat-tail at PGI, PGM, EST-1, EST-2, and G6PDH ($p<0.05$) (Table 4). In populations of *D. julianalis* sampled from musk thistle, only EST-1, EST-2, G6PDH, MDH-2, and 6PGD were heterogeneous ($p<0.05$) (Table 5). Several loci from populations of *D. julianalis* collected from the common bagworm exhibited significant heterogeneity ($p<0.05$)(PGM, EST-1, EST-2, EST-4, and MDH-2) (Table 6). Significant heterogeneity among these populations indicate that significant variation exists across Tennessee in populations of *D. julianalis* sampled from the same host.

Table 4. Allele frequencies of nine populations of *Dicymolomia julianalis* (Walker) collected from cat-tail in Tennessee, 1994.

Locus	Cat-tail Populations									Chi-Square	df	P
	1*	2	3	4	5	6	7	8	9			
PGI												
(n)	30	30	30	30	30	30	30	30	30			
A	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.003			
B	0.050	0.117	0.067	0.300	0.233	0.133	0.100	0.233	0.100			
C	0.850	0.783	0.883	0.600	0.633	0.817	0.850	0.733	0.833			
D	0.100	0.100	0.050	0.100	0.133	0.033	0.050	0.033	0.033	52.3	24	0.00073
PGM												
(n)	30	30	30	30	29	30	30	30	30			
A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
B	0.067	0.117	0.050	0.017	0.017	0.033	0.033	0.017	0.017			
C	0.183	0.267	0.167	0.150	0.310	0.150	0.217	0.300	0.167			
D	0.733	0.167	0.650	0.717	0.517	0.800	0.600	0.633	0.783			
E	0.017	0.650	0.133	0.117	0.155	0.017	0.050	0.050	0.033	53.1	24	0.00056
GPDH												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
EST-1												
(n)	25	29	30	27	30	30	29	30	28			
A	0.080	0.224	0.483	0.333	0.467	0.517	0.552	0.500	0.393			
B	0.920	0.776	0.517	0.667	0.533	0.483	0.448	0.500	0.607	44.1	8	0.0001
EST-2												
(n)	30	30	30	30	30	30	29	30	29			
A	0.000	0.000	0.067	0.067	0.100	0.000	0.034	0.050	0.052			
B	0.600	0.650	0.433	0.467	0.500	0.467	0.655	0.483	0.448			
C	0.400	0.350	0.500	0.467	0.400	0.533	0.310	0.467	0.500	27.9	16	0.0329
EST-3												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
EST-4												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			

Table 4. continued

Locus	Cat-tail Populations 1	2	3	4	5	6	7	8	9	Chi-Square	df	P
G6PDH												
(n)	30	30	30	30	30	30	30	30	30			
A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
B	0.650	0.833	0.917	0.700	0.517	0.833	0.667	0.767	0.600			
C	0.350	0.167	0.083	0.283	0.483	0.167	0.333	0.233	0.400			
D	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	46.9	16	0.0007
MDH-1												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
MDH-2												
(n)	30	30	30	30	30	30	30	30	30			
A	0.017	0.067	0.050	0.117	0.083	0.000	0.067	0.000	0.050			
B	0.983	0.933	0.933	0.883	0.917	1.000	0.933	1.000	0.950			
C	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000	23.5	16	0.10208
ME												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
HK-1												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
HK-2												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
6PGD												
(n)	30	30	30	30	30	30	30	30	30			
A	0.633	0.783	0.733	0.683	0.717	0.833	0.783	0.800	0.867			
B	0.367	0.217	0.267	0.317	0.283	0.167	0.217	0.200	0.133	14.4	16	0.07129

*Population site location (County): 1=Washington, 2=Greene, 3=Knox, 4=Putnam, 5=Cumberland, 6=Marshall, 7=Madison, 8=Crockett, and 9=Henry

Table 5. Allele frequencies of six populations of *Dicymolomia julianalis* (Walker) collected from musk thistle in Tennessee, 1994.

Locus	Musk Thistle Populations						Chi-Square	df	P
	10*	11	12	13	14	15			
PGI									
(n)	30	30	30	30	30	30			
A	0.000	0.017	0.000	0.000	0.000	0.000			
B	0.183	0.083	0.150	0.150	0.133	0.133			
C	0.783	0.800	0.750	0.717	0.800	0.800			
D	0.033	0.100	0.100	0.133	0.067	0.067	12.2	15	0.66518
PGM									
(n)	30	29	30	30	28	30			
A	0.000	0.000	0.000	0.000	0.000	0.000			
B	0.000	0.034	0.067	0.067	0.000	0.067			
C	0.283	0.310	0.250	0.317	0.321	0.350			
D	0.700	0.603	0.550	0.567	0.643	0.517			
E	0.017	0.052	0.133	0.050	0.036	0.067	19.5	15	0.19285
GPDH									
(n)	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000			
EST-1									
(n)	30	30	29	30	30	30			
A	0.500	0.717	0.621	0.650	0.0617	0.450			
B	0.500	0.283	0.379	0.350	0.383	0.550	12.2	5	0.03268
EST-2									
(n)	30	30	29	30	30	30			
A	0.000	0.000	0.000	0.000	0.000	0.000			
B	0.367	0.350	0.414	0.600	0.550	0.467			
C	0.633	0.650	0.586	0.400	0.450	0.533	12.2	5	0.03178
EST-3									
(n)	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000			
EST-4									
(n)	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000			

Table 5 continued

Locus	Musk Thistle Populations						Chi-Square	df	P
	10	11	12	13	14	15			
G6PDH									
(n)	28	30	30	30	30	30			
A	0.000	0.000	0.000	0.017	0.083	0.017			
B	0.732	0.617	0.800	0.717	0.633	0.667			
C	0.268	0.383	0.200	0.267	0.283	0.317	21.8	10	0.01620
MDH-1									
(n)	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000			
MDH-2									
(n)	30	30	30	30	30	30			
A	0.033	0.000	0.033	0.100	0.000	0.000			
B	0.933	1.000	0.900	0.867	0.983	0.950			
C	0.033	0.000	0.067	0.033	0.017	0.050	22.2	10	0.01409
ME									
(n)	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000			
HK-1									
(n)	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000			
HK-2									
(n)	30	30	30	30	30	30			
A	0.967	0.967	0.983	1.000	0.967	0.967			
B	0.033	0.033	0.017	0.000	0.033	0.033	2.4	5	0.79249
6PGD									
(n)	30	30	30	30	30	30			
A	0.150	0.050	0.217	0.133	0.100	0.183			
B	0.850	0.950	0.783	0.850	0.900	0.733			
C	0.000	0.000	0.000	0.017	0.000	0.083	29.8	10	0.00094

* Population site location (County): 10=Jefferson, 11=Knox, 12=Greene, 13=Wilson, 14=Davidson, and 15=Rutherford

Table 6. Allele frequencies of nine populations of *Dicymolomia julianalis* (Walker) collected from the common bagworm in Tennessee, 1995.

Locus	Common Bagworm Populations									Chi-Square	df	P
	16*	17	18	19	20	21	22	23	24			
PGI												
(n)	30	30	30	30	30	30	30	30	29			
A	0.050	0.050	0.033	0.000	0.000	0.000	0.000	0.000	0.000			
B	0.067	0.100	0.083	0.067	0.033	0.050	0.117	0.133	0.069			
C	0.883	0.850	0.833	0.917	0.967	0.900	0.800	0.833	0.879			
D	0.000	0.000	0.050	0.017	0.000	0.050	0.067	0.033	0.052			
E	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	43.2	32	0.08884
PGM												
(n)	30	30	28	30	30	30	30	30	30			
A	0.033	0.033	0.036	0.000	0.000	0.000	0.000	0.050	0.000			
B	0.050	0.017	0.125	0.000	0.000	0.083	0.050	0.100	0.067			
C	0.167	0.333	0.286	0.217	0.233	0.200	0.167	0.167	0.167			
D	0.600	0.567	0.500	0.550	0.650	0.450	0.583	0.483	0.650	65.5	40	0.00663
GPDH												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
EST-1												
(n)	30	30	30	30	30	30	30	30	30			
A	0.200	0.267	0.483	0.300	0.433	0.500	0.517	0.417	0.333			
B	0.733	0.717	0.517	0.617	0.517	0.467	0.450	0.517	0.567			
C	0.050	0.017	0.000	0.083	0.050	0.033	0.033	0.067	0.100			
D	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	42.8	24	0.01050
EST-2												
(n)	30	30	30	30	30	30	30	30	30			
A	0.000	0.000	0.000	0.050	0.083	0.000	0.033	0.050	0.000			
B	0.717	0.650	0.483	0.517	0.500	0.450	0.600	0.450	0.367			
C	0.233	0.317	0.500	0.417	0.400	0.500	0.317	0.433	0.550			
D	0.050	0.033	0.017	0.017	0.017	0.050	0.050	0.067	0.083	49.5	24	0.00100
EST-3												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
EST-4												
(n)	30	30	30	30	30	30	30	30	30			
A	0.933	1.000	1.000	0.883	1.000	0.983	1.000	0.983	0.950			

Table 6 continued

Locus	Common Bagworm Populations									Chi-Square	df	P
	16	17	18	19	20	21	22	23	24			
EST-4												
B	0.067	0.000	0.000	0.117	0.000	0.017	0.000	0.017	0.050	27.6	8	0.00056
G6PDH												
(n)	30	28	30	30	30	30	30	29	30			
A	0.000	0.000	0.033	0.000	0.000	0.000	0.000	0.017	0.017			
B	0.750	0.643	0.600	0.850	0.767	0.700	0.683	0.621	0.683			
C	0.250	0.339	0.350	0.150	0.233	0.300	0.317	0.345	0.300			
D	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.017	0.000			
E	0.000	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	36.3	32	0.27341
MDH-1												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
MDH-2												
(n)	30	30	30	30	30	30	30	30	30			
A	0.000	0.000	0.033	0.000	0.000	0.017	0.000	0.0000	0.000			
B	0.983	1.000	0.950	0.933	1.000	0.983	0.983	1.000	1.000			
C	0.017	0.000	0.017	0.067	0.000	0.000	0.017	0.000	0.000	29.7	16	0.01954
ME												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
HK-1												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
HK-2												
(n)	30	30	30	30	30	30	30	30	30			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
6PGD												
(n)	30	30	30	30	30	30	30	30	30			
A	0.217	0.217	0.217	0.300	0.133	0.283	0.217	0.150	0.167			
B	0.783	0.783	0.783	0.700	0.867	0.717	0.783	0.833	0.833			
C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	16.9	16	0.39375

*Population site location (County): 16=Jefferson, 17=Knox, 18=Greene, 19=Smith, 20=Wilson, 21=Davidson, 22=Madison, 23=Crockett, and 24=Haywood

Table 7. Mean allele frequencies of all loci from populations of *Dicymolomia julianalis* (Walker) collected from cat-tail, musk thistle, and the common bagworm in Tennessee, 1994 and 1995.

Locus	Hosts			Chi-Square	df	P
	Cat-tail	Musk-thistle	Common Bagworm			
PGI						
(n)	270	180	269			
A	0.006	0.003	0.015			
B	0.148	0.139	0.080			
C	0.776	0.775	0.874			
D	0.070	0.083	0.030			
E	0.000	0.000	0.002	34.7	8	0.00003
PGM						
(n)	269	177	268			
A	0.000	0.000	0.017			
B	0.052	0.040	0.054			
C	0.212	0.305	0.215			
D	0.664	.0596	0.560			
E	0.072	0.059	0.140			
F	0.000	0.000	0.015	62.8	1	0.00001
GPDH						
(n)	270	180	270			
A	1.000	1.000	1.000			
EST-1						
(n)	258	179	270			
A	0.401	0.592	0.383			
B	0.599	0.408	0.567			
C	0.000	0.000	0.048			
D	0.000	0.000	0.002	83.7	6	0.00001
EST-2						
(n)	268	179	270			
A	0.041	0.000	0.024			
B	0.522	0.458	0.526			
C	0.437	0.542	0.407			
D	0.000	0.000	0.043	64.3	6	0.00001
EST-3						
(n)	270	180	270			
A	1.000	1.000	1.000			
EST-4						
(n)	270	180	270			
A	1.000	1.000	0.970			
B	0.000	0.000	0.030	27.0	2	0.00001
G6PDH						
(n)	270	178	267			
A	0.000	0.020	0.007			
B	0.720	0.694	0.700			
C	0.278	0.287	0.287			
D	0.002	0.000	0.004			
E	0.002	0.000	0.002	14.26	8	0.07508
MDH-1						
(n)	270	180	270			
A	1.000	1.000	1.000			

Table 7 continued

Locus	Host			Chi-Square	df	P
	Cat-tail	Musk Thistle	Common Bagworm			
MDH-2						
(n)	270	180	270			
A	0.050	0.028	0.006			
B	0.948	0.939	0.981			
C	0.002	0.033	0.013	35.2	4	0.00001
ME						
(n)	270	180	270			
A	1.000	1.000	1.000			
HK-1						
(n)	270	180	270			
A	1.000	1.000	1.000			
HK-2						
(n)	270	180	270			
A	1.000	0.975	1.000			
B	0.000	0.025	0.000	27.2	2	0.00001
6PGD						
(n)	270	180	270			
A	0.759	0.139	0.211			
B	0.241	0.844	0.787			
C	0.000	0.017	0.002	483.2	4	0.00001

When mean allele frequencies for each host were compared, all loci except G6PDH were found to be significantly heterogeneous ($p<0.05$) (Table 7). This result indicates differences exist in allele frequencies among populations of *D. julianalis* collected from cat-tail, musk thistle, and the common bagworm. Significant heterogeneity of allele frequency exists among populations on different hosts, which is indicative of genetic differentiation of populations on each host.

Other genetic studies of host races have demonstrated significant heterogeneity of allele frequencies. Sturgeon and Mitton (1986) reported that two of five polymorphic loci examined were significantly heterogeneous in mountain pine beetles, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Feder *et al.* 1988 and McPheron *et al.* 1988 reported six of 13 and two of 10 loci, respectively as significantly heterogeneous in host races of *Rhagoletis pomonella.* Waring *et al.* 1990 reported genetic differentiation in the gallformer *Eurosta solidaginis* along host lines at two of the six polymorphic loci examined. More heterogeneity in allele frequencies of *D. julianalis* from different hosts is reported here than in previous studies of host races.

The greatest differentiation of allele frequencies for populations of *D. julianalis* collected from each host was realized at the 6PGD locus (Table 7). In cat-tail populations allele A was most frequent; however, in musk thistle and common bagworm populations allele B was in highest frequency. The presence of uncommon alleles also is important in explaining the differences in allele

frequencies. Allele E of PGI was only found only in common bagworm populations. At the PGM locus allele F was present only in common bagworm populations. At the EST-1 locus alleles C and D were present only in common bagworm populations. The D allele at EST-2 also was uncommon and present only in common bagworm populations. EST-4 was monomorphic in cat-tail and musk thistle populations; however, a second allele was present in common bagworm populations. At the G6PDH locus, alleles D and E were present only in cat-tail and common bagworm populations, and allele A was present only in common bagworm populations. HK-2 was monomorphic in cat-tail and common bagworm populations, however, in musk thistle populations a second allele was present. Allele C of 6PGD was present in musk thistle and common bagworm populations, but not in cat-tail populations. The presence of alleles in populations from one host, but not in others is indicative of a reduction in migration among those hosts.

The average level of polymorphism, when all populations were analyzed, was 50.9 percent (range 42.9 to 57.2), the mean number of alleles was 2.03 (range 1.7 to 2.3), and heterozygosity averaged 0.157 (range 0.119 to 0.211). When only populations of *D. julianalis* from cat-tail were analyzed, the average level of polymorphism was 48.4 percent (range 42.9 to 50.0 percent), the mean number of alleles was 1.8 (range 1.7 to 1.9), and heterozygosity averaged 0.155 (range 0.119 to 0.189). For musk thistle populations, the mean level of polymorphism was 54.7 percent (range 50.0 to 57.1), the average number of alleles was 1.9 (range 1.8

to 1.9), and heterozygosity averaged 0.159 (range 0.135 to 0.198). When populations of *D. julianalis* from the common bagworm were analyzed, the mean level of polymorphism was 50.8 percent (range 42.9 to 57.1), the average number of alleles was 2.02 (range 1.7 to 2.3), and heterozygosity averaged 0.157 (range 0.129 to 0.211). Values of heterozygosity, number of alleles at each locus, and polymorphism were similar among populations collected from cat-tail, musk thistle, and common bagworm.

Nevo *et al.* (1984) reported levels of heterozygosity and polymorphism in *Drosophila* spp. (n=34 species) as 0.123 (±0.053) and 48.0 percent (±14.3), respectively. Insects (n=95 species), excluding hymenopterans and *Drosophila* spp., had an average heterozygosity of 0.103 (±0.058), and 39.8 percent (±17.4) of the loci surveyed were polymorphic (Nevo *et al.* 1984). Thus, values of heterozygosity and polymorphism in *D. julianalis* are somewhat higher than means reported for selected insects and *Drosophila* spp. However, most values reported here for populations of *D. julianalis* do fall within one standard deviation of the values reported for other insect species. These values indicate that a large amount of genetic variation exists in populations of *D. julianalis*.

A total of 172 (61 loci in cat-tail populations, 46 loci in musk thistle populations, and 65 loci in bagworm populations) chi-square tests was performed to examine goodness of fit to Hardy-Weinberg expectations. Only 25 loci indicated a significant deviation from Hardy-Weinberg at the 0.05 level of significance. All of the loci differing from Hardy-Weinberg displayed a

heterozygote deficiency (positive fixation index). Deficiencies in heterozygotes can be caused by several factors: 1) presence of null or silent alleles, 2) selection against heterozygotes, 3) emergence of heterozygotes before homozygotes, 4) Walhund effect, when one sampled locality supports two or more subpopulations (e.g., adapted to different hosts), and 5) inbreeding (Sturgeon and Mitton 1986). The presence of null or silent alleles is improbable because most of the loci studied were well resolved. Selection is less likely to be evoked simply because allozyme markers are considered neutral and not indicative of the effects of selection. Differential emergence time also is contrary to expectation because larvae were collected prior to emergence. The Walhund effect also is improbable because collections were made from each host. Therefore, the observed heterozygote deficiencies are most likely attributable to local inbreeding within populations on each host. Local inbreeding occurs when a high frequency of mating is among related individuals and is generally attributed to small population sizes.

F-statistics are a method which partition the distribution of genetic variation into components due to inbreeding (F_{IS}) and population structure (F_{ST}). F_{IS} and F_{IT} measure departures from Hardy-Weinberg as a result of non-random mating within subpopulations and across populations, respectively. Amounts of genetic structuring among populations, as measured by F_{ST}, of a species are generally associated with vagility of the organism. Active dispersers generally have low values of F_{ST}, while sedentary species have higher ones (McCauley and

Eanes 1987). In general, genetic drift and selection act to diversify population structure, while gene flow is a homogenizing force making populations more similar.

When all 24 populations were pooled into a single analysis, the average levels of inbreeding for all loci within populations (F_{IS}) was 0.177 (Table 8). This value measures the deviation from Hardy-Weinberg proportions within each subpopulation, as a result of non-random mating. The fixation index (F_{ST}) was 0.095 (Table 8), this relatively high value is indicative of genetic structuring at the population level. F_{IT} for these populations was 0.255 and is the sum of F_{ST} and F_{IS} and represents the total departure from Hardy-Weinberg in the whole population due to inbreeding within populations as well as population subdivision.

To determine if the primary source of this apparent structure was host plant or geographic location, the data were analyzed with all populations from each host grouped into separate analyses. Estimates of inbreeding within populations (F_{IS}) from all hosts were similar to estimates when all populations were combined (Tables 8, 9, 10, and 11), which indicates that the host from which samples were collected has no impact on the level of inbreeding within populations. The amount of inbreeding is most likely caused by small population sizes which promotes the probability of mating with a related individual.
The value of F_{ST} for populations of *D. julianalis* collected from cat-tail, musk thistle, and common bagworm were 0.048 (Table 9), 0.023 (Table 10), and 0.029

Table 8. Summary of F-statistics at all loci from 24 populations of *Dicymolomia julianalis* (Walker) collected from cat-tail, musk thistle, and common bagworm in Tennessee, 1994 and 1995.

Locus	F(IS)	F(IT)	F(ST)
PGI	0.021	0.059	0.039
PGM	0.163	0.190	0.033
EST-1	0.191	0.259	0.084
EST-2	0.154	0.188	0.040
EST-4	0.186	0.242	0.069
G6PDH	0.171	0.204	0.039
MDH-2	-0.041	0.001	0.040
HK-2	-0.032	-0.006	0.025
6PGD	0.435	0.625	0.336
Mean	0.177	0.255	0.095

Table 9. Summary of F-statistics at all loci from nine populations of *Dicymolomia julianalis* (Walker) collected from cat-tail in Tennessee, 1994.

Locus	F(IS)	F(IT)	F(ST)
PGI	0.069	0.112	0.046
PGM	0.084	0.115	0.034
EST-1	0.146	0.224	0.091
EST-2	0.086	0.108	0.024
G6PDH	0.309	0.358	0.072
MDH-2	-0.083	-0.053	0.028
6PGD	0.480	0.493	0.027
Mean	0.172	0.212	0.048

Table 10. Summary of F-statistics at all loci from six populations of *Dicymolomia julianalis* (Walker) collected from musk thistle in Tennessee, 1994.

Locus	F(IS)	F(IT)	F(ST)
PGI	-0.096	-0.087	0.008
PGM	0.109	0.121	0.013
EST-1	0.232	0.258	0.034
EST-2	0.301	0.325	0.034
G6PDH	0.237	0.250	0.018
MDH-2	0.015	0.047	0.033
HK-2	-0.033	-0.026	0.007
6PGD	0.355	0.377	0.033
Mean	0.174	0.193	0.023

Table 11. Summary of F-statistics at all loci from nine populations of *Dicymolomia julianalis* (Walker) collected from the common bagworm in Tennessee, 1995.

Locus	F(IS)	F(IT)	F(ST)
PGI	0.075	0.093	0.019
PGM	0.259	0.276	0.022
EST-1	0.205	0.238	0.041
EST-2	0.132	0.166	0.039
EST-4	0.186	0.227	0.051
G6PDH	0.003	0.026	0.022
MDH-2	-0.045	-0.015	0.029
6PGD	0.429	0.438	0.016
Mean	0.185	0.208	0.029

(Table 11), respectively. All of the F_{ST} values for each host were lower when analyzed separately, which indicates that genetic structure in the populations can be attributed to differentiation on hosts. The F_{ST} value is highest in populations of *D. julianalis* collected from cat-tail (0.048), and may be due to the more patchydistribution (because it is confined to wet areas) than musk thistle or common bagworm, which have somewhat more continuous distributions. Because of the patchy distribution of cat-tail, genetic drift has more of an effect on those populations and has lead to more geographic structuring.

Gene flow or the effective migration rate (Nm) was calculated using F_{ST} values (Slatkin and Barton 1989 and Cockerham and Weir 1993). Parameters estimating migration are not precise and represent relative estimates of gene flow. When all populations were analyzed without regard to host, the mean level of gene flow estimated between all populations was relatively low (Nm=2.38). The 6PGD locus (Nm=0.494) demonstrated the greatest restriction in gene flow. These data indicate that some factor(s) is limiting the amount of genetic exchange among these populations. Gene flow estimates among populations of cat-tail (Nm=4.96), musk thistle (Nm=10.62), and common bagworm (Nm=8.37) are all greater, indicating that more gene flow occurs within these populations on each host than among populations from different hosts.

To ascertain levels of gene flow between populations of *D. julianalis* on each host, hierarchical F_{ST} values were calculated to estimate Nm. The greatest amount of gene flow was realized between populations collected from the

common bagworm and musk thistle (Nm=10.62). However, gene flow was more restricted between cat-tail-musk thistle analysis (Nm=2.53) and the cat-tail-common bagworm analysis (Nm=3.03). Slatkin and Barton (1989) reported that unless Nm is less than one, genetic drift can not lead to the fixation of alternative alleles, thus differentiation among populations is less likely. These values reported are close to one, indicating a reduction in gene flow occurs between populations on each host. Another symptom of reduced gene flow is that more gene flow exists across Tennessee on each host, than within an area that contains each host. The fact that values of Nm are larger than one may represent the relatively recent divergence of these populations, and thus, the apparent presence of gene flow may actually be an artifact of gene flow in the past.

Another method was undertaken to estimate the level of migration between populations of *D. julianalis* on cat-tail, musk thistle, and common bagworm. This method consisted of examining the correlation of allele frequencies for all polymorphic loci between sympatric sites for each host. The correlation coefficient of allele frequencies between sympatric populations of *D. julianalis* sampled from cat-tail and musk thistle was 0.139 and was not different from 0 ($P>0.05$). The lack of association of allele frequencies between these sympatric populations of *D. julianalis* indicates that little migration occurs between these populations. The same trend was evident in the correlation of allele frequencies ($r=0.058$) between sympatric populations of *D. julianalis* collected from cat-tail and common bagworm. However, a significant association of alleles

(r=0.792) between populations of *D. julianalis* sampled from musk thistle and common bagworm did exist. These results indicate that little migration among populations of *D. julianalis* on cat-tail and common bagworm, populations from cat-tail and musk thistle, and more migration among populations of *D. julianalis* on common bagworm and musk thistle.

Genetic similarity (Rogers 1972) and Modified Rogers genetic distances (Wright 1978) were calculated for all 24 populations (Table 12). Coefficients of genetic distances and similarity also were calculated for each group of host populations (Tables 13, 14, and 15). The mean similarity within cat-tail populations was 0.941 (range 0.916 to 0.969) (Table 13), while the average similarity within musk thistle populations was 0.956 (range 0.943 to 0.965) (Table14), and the mean similarity within bagworm populations was 0.952 (range 0.933 to 0.968) (Table 15). Host populations also were pooled to obtain an overall estimate of similarity and distance among populations collected from each host. Cat-tail populations had genetic similarity values of 0.924 and 0.936 to musk thistle and common bagworm populations, respectively, and musk thistle and bagworm populations had a similarity of 0.954. Genetic distance between pooled cat-tail populations and musk thistle populations and common bagworm populations were 0.175 and 0.152, respectively, while pooled musk thistle and common bagworm populations had a genetic distance of 0.072. These values of genetic similarity and distance indicate that populations of *D. julianalis* from cat-tail are most different from those collected from common bagworm and musk

Table 12. Similarity and distance measures of all populations of *Dicymolomia julianalis* (Walker) from cat-tail, musk thistle, and common bagworm in Tennessee, 1994 and 1995. Rogers genetic similarity coefficients are listed below diagonal of asterisks, while the Modified Rogers distances are listed above diagonal of asterisks.

Population	1*	2	3	4	5	6	7	8	9	10	11	12
1	*****	0.090	0.141	0.108	0.139	0.144	0.139	0.138	0.114	0.188	0.244	0.201
2	0.942	*****	0.099	0.096	0.122	0.113	0.102	0.096	0.110	0.207	0.258	0.197
3	0.921	0.942	*****	0.102	0.130	0.059	0.094	0.071	0.101	0.173	0.216	0.154
4	0.906	0.936	0.941	*****	0.083	0.099	0.108	0.080	0.089	0.165	0.218	0.162
5	0.916	0.928	0.935	0.951	*****	0.127	0.088	0.086	0.097	0.181	0.208	0.169
6	0.921	0.938	0.962	0.933	0.921	*****	0.088	0.056	0.074	0.191	0.232	0.180
7	0.934	0.953	0.948	0.932	0.944	0.948	*****	0.071	0.085	0.194	0.222	0.175
8	0.922	0.944	0.956	0.948	0.948	0.969	0.955	*****	0.077	0.180	0.220	0.167
9	0.937	0.932	0.947	0.947	0.940	0.962	0.949	0.951	*****	0.202	0.242	0.201
10	0.893	0.887	0.915	0.910	0.901	0.917	0.905	0.926	0.906	*****	0.079	0.061
11	0.876	0.860	0.883	0.873	0.885	0.886	0.891	0.895	0.886	0.952	*****	0.082
12	0.882	0.900	0.920	0.905	0.904	0.915	0.909	0.920	0.892	0.960	0.946	*****
13	0.892	0.900	0.897	0.905	0.908	0.893	0.918	0.912	0.884	0.949	0.944	0.961
14	0.897	0.886	0.899	0.893	0.900	0.905	0.914	0.918	0.896	0.959	0.961	0.953
15	0.908	0.905	0.917	0.913	0.920	0.914	0.918	0.925	0.915	0.962	0.943	0.956
16	0.919	0.918	0898	0.899	0.880	0.886	0.904	0.894	0.889	0.918	0.892	0.919
17	0.931	0.922	0.895	0.908	0.904	0.893	0.919	0.909	0.908	0.931	0.920	0.924
18	0.911	0.905	0.922	0.909	0.923	0.913	0.927	0.922	0.922	0.955	0.943	0.955
19	0.905	0.916	0.925	0.907	0.896	0.904	0.899	0.907	0.897	0.920	0.891	0.932
20	0.905	0.898	0.923	0.906	0.901	0.912	0.910	0.924	0.904	0.953	0.931	0.941
21	0.908	0.899	0.928	0.909	0.913	0.916	0.924	0.922	0.910	0.944	0.929	0.950
22	0.914	0.908	0.917	0.910	0.915	0.913	0.937	0.922	0.907	0.948	0.933	0.953
23	0.905	0.895	0.910	0.906	0.913	0.904	0.914	0.914	0.911	0.947	0.937	0.941
24	0.913	0.892	0.917	0.911	0.892	0.907	0.905	0.908	0.912	0.953	0.936	0.939

Table 12 continued

Population	13	14	15	16	17	18	19	20	21	22	23	24
1	0.211	0.208	0.164	0.137	0.134	0.167	0.145	0.178	0.169	0.172	0.176	0.163
2	0.210	0.211	0.177	0.163	0.165	0.182	0.150	0.197	0.173	0.181	0.195	0.194
3	0.185	0.193	0.161	0.179	0.180	0.166	0.134	0.170	0.142	0.162	0.178	0.170
4	0.180	0.189	0.152	0.167	0.160	0.158	0.147	0.180	0.154	0.156	0.167	0.164
5	0.176	0.186	0.151	0.186	0.165	0.152	0.168	0.191	0.149	0.155	0.167	0.180
6	0.206	0.210	0.183	0.205	0.200	0.187	0.171	0.198	0.173	0.184	0.203	0.193
7	0.180	0.192	0.167	0.181	0.173	0.163	0.164	0.187	0.153	0.156	0.182	0.190
8	0.188	0.195	0.163	0.192	0.180	0.169	0.160	0.190	0.158	0.168	0.186	0.185
9	0.220	0.221	0.187	0.204	0.193	0.187	0.182	0.208	0.180	0.191	0.204	0.196
10	0.086	0.068	0.061	0.137	0.112	0.071	0.110	0.078	0.091	0.092	0.085	0.067
11	0.089	0.068	0.098	0.183	0.155	0.092	0.159	0.111	0.108	0.112	0.105	0.110
12	0.064	0.073	0.068	0.146	0.130	0.073	0.105	0.089	0.069	0.081	0.085	0.091
13	*****	0.050	0.079	0.138	0.118	0.076	0.125	0.093	0.094	0.067	0.092	0.112
14	0.965	*****	0.071	0.133	0.107	0.067	0.123	0.074	0.092	0.067	0.081	0.093
15	0.948	0.958	*****	0.113	0.080	0.037	0.091	0.076	0.064	0.073	0.061	0.069
16	0.918	0.918	0.926	*****	0.056	0.111	0.076	0.091	0.114	0.093	0.099	0.103
17	0.935	0.940	0.951	0.965	*****	0.080	0.090	0.082	0.101	0.083	0.084	0.091
18	0.949	0.955	0.973	0.934	0.957	*****	0.098	0.074	0.055	0.063	0.049	0.067
19	0.914	0.915	0.934	0.949	0.936	0.933	*****	0.076	0.078	0.090	0.089	0.082
20	0.943	0.952	0.948	0.946	0.948	0.952	0.948	*****	0.074	0.064	0.066	0.062
21	0.936	0.941	0.958	0.934	0.940	0.966	0.949	0.954	*****	0.063	0.053	0.072
22	0.955	0.958	0.957	0.952	0.959	0.964	0.937	0.958	0.964	*****	0.055	0.083
23	0.940	0.950	0.959	0.938	0.952	0.968	0.938	0.962	0.966	0.964	*****	0.056
24	0.930	0.940	0.951	0.947	0.947	0.954	0.944	0.961	0.958	0.953	0.966	*****

*Population site location (County): 1=Washington, 2=Greene, 3=Knox, 4=Putnam, 5=Cumberland, 6=Marshall, 7=Madison, 8=Crockett, 9=Henry, 10=Jefferson, 11=Knox, 12=Greene, 13=Wilson, 14=Davidson, 15=Rutherford, 16=Jefferson, 17=Knox, 18=Greene, 19=Smith, 20=Wilson, 21=Davidson, 22=Madison, 23=Crockett, and 24=Haywood

Table 13. Rogers genetic similarity for populations of *Dicymolomia julianalis* (Walker) collected from cat-tail in Tennessee, 1994.

Pop.#	1	2	3	4	5	6	7	8	9
1	*****								
2	0.942	*****							
3	0.921	0.942	****						
4	0.935	0.936	0.941	****					
5	0.916	0.928	0.935	0.951	****				
6	0.921	0.938	0.962	0.933	0.921	****			
7	0.934	0.953	0.948	0.932	0.944	0.948	****		
8	0.922	0.944	0.956	0.948	0.948	0.969	0.955	****	
9	0.937	0.932	0.947	0.947	0.940	0.962	0.949	0.951	****

#=Population

*Population site location (County): 1=Washington, 2=Greene, 3=Knox, 4=Putnam, 5=Cumberland, 6=Marshall, 7=Madison, 8=Crockett, and 9=Henry

Table 14. Rogers genetic similarity for populations of *Dicymolomia julianalis* (Walker) collected from musk thistle in Tennessee, 1994.

Pop.#	10*	11	12	13	14	15
10	****					
11	0.952	*****				
12	0.960	0.946	*****			
13	0.949	0.944	0.961	*****		
14	0.959	0.961	0.953	0.965	*****	
15	0.962	0.943	0.956	0.948	0.958	*****

#=Population

*Population site location (County): 10=Jefferson, 11=Knox, 12=Greene, 13=Wilson, 14=Davidson, and 15=Rutherford

Table 15. Rogers genetic similarity for populations of *Dicymolomia julianalis* (Walker) collected from common bagworm in Tennessee, 1995.

Pop.#	16*	17	18	19	20	21	22	23	24
16	*****								
17	0.965	*****							
18	0.934	0.957	****						
19	0.949	0.936	0.933	****					
20	0.946	0.948	0.952	0.948	****				
21	0.934	0.940	0.966	0.949	0.954	****			
22	0.952	0.959	0.964	0.937	0.958	0.964	****		
23	0.938	0.952	0.968	0.938	0.962	0.966	0.964	****	
24	0.947	0.947	0.954	0.944	0.961	0.958	0.953	0.966	****

#=Population

*Population site location (County): 16=Jefferson, 17=Knox, 18=Greene, 19=Smith, 20=Wilson, 21=Davidson, 22=Madison, 23=Crockett, and 24=Haywood

thistle. Musk thistle and common bagworm populations are more similar to each other than both are to cat-tail populations.

Other measures of genetic distance and similarity also were calculated. Nei's (1972) genetic distance values for populations of *D. julianalis* from cat-tail and musk thistle were 0.047 (i.e., 95% similar), cat-tail and common bagworm 0.037 (i.e., 96% similar), while musk thistle and common bagworm populations were 0.014 (i.e., 98% similar). Again, these results are quantitatively and qualitatively similar to those reported above. As mentioned previously, few studies have attempted to recognize host races using allozymes, and even fewer have calculated measures of similarity and distance. Sturgeon and Mitton (1986) reported that the mountain pine beetle *Dendroctonus ponderosae* was genetically differentiated on three pine hosts, and values of Nei's genetic identity all exceeded 0.99. Waring *et al.* (1990) displayed a phenogram of Nei's genetic distances among populations of the gallformer *Eurosta solidaginis* on two species of *Solidago*. The level of genetic distance between the two host races was approximately 0.032 (i.e., 97% similar). These values reported for *D. julianalis* do appear to be of the same magnitude as other possible host races, although the values realized among host populations of *D. julianalis* are more differentiated.

A phenogram was generated utilizing the algorithm of unweighted pair grouping method analysis for Modified Rogers genetic distances (Figure 6) to examine the evolutionary relationship among populations of *D. julianalis*. The resulting phenogram had a cophenetic correlation of 0.923 indicating that the data

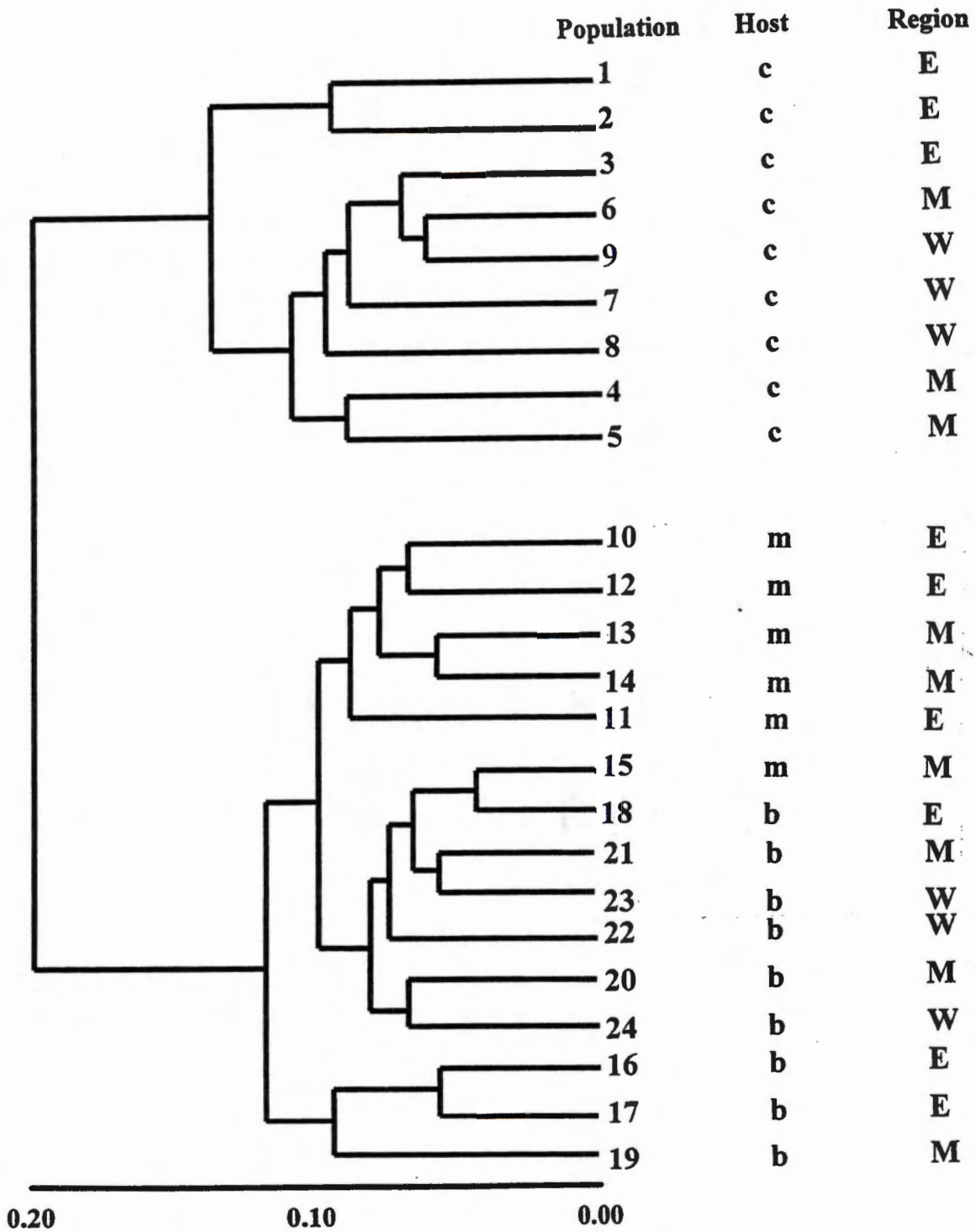


Figure 6. Phenogram generated by UPGMA of Modified Rogers genetic distances among populations of *Dicymolomia julianalis* (Walker) sampled from cat-tail (c), musk thistle (m), and common bagworm (b) collected from eastern (E), middle (M), and western (W) Tennessee in 1994 and 1995. Population number refers to specific location of site.

did fit the tree well. All populations of *D. julianalis* cluster according to the host from which the larvae were sampled, with the exception of one population sampled from musk thistle in middle Tennessee (Rutherford Co.). The greatest genetic

distance (0.182) was realized between cat-tail and the two other hosts of *D. julianalis*. The split between musk thistle populations and cat-tail occurred at a distance of 0.109. The characteristics of the phenogram overall indicate that populations of *D. julianalis* from each host are more similar to each other, than populations collected from the same geographic location, even when sites are in close proximity.

These data accumulated from allozyme analysis (allele frequencies, F-statitics, estimates of migration, and genetic distances and similarities) support the conclusion that populations of *D. julianalis* collected from different hosts are distinct genetically. It is also apparent that populations of *D. julianalis* are partially reproductively isolated and thus represent putative host races.

CHAPTER IV

CONCLUSIONS

Analysis of allozyme data indicate that *Dicymolomia julianalis* is partially reproductively isolated from conspecific populations on different hosts. As a result, *D. julianalis* should be classified as having host races. Several avenues of results have led to this conclusion: significant differences in allele frequencies exist at eight of nine polymorphic loci, analyses of population structure, effective migration, and analyses of the evolutionary relationships among *D. julianalis* sampled from different hosts.

A primary goal of this research was to ascertain levels of genetic variation and its distribution in populations of *D. julianalis* sampled from cat-tail, musk thistle, and common bagworm. Results indicate that high levels of polymorphism and heterozygosity exist in populations of *D. julianalis* on each host. Significant heterogeneity in allele frequencies exists among populations on different hosts at eight of nine polymorphic loci examined. These levels of differentiation at polymorphic loci are higher than in other studies which have indicated the existence of host races (Feder *et al.* 1988, McPheron *et al.* 1988, Sturgeon and Mitton 1986, and Waring *et al.* 1990).

One alternative hypothesis to the existence of host races is that adult moths are mating panmicticly and interhost divergence is generated by differential

selection acting on genes closely linked to the enzyme loci in question. The most direct test would be to sample adult moths, preferably ones that are mating and ovipositing. In this experiment, if selection were causing differences in allele frequencies among hosts, then analyses of adult populations should show allele frequencies to be homogeneous. However, allele frequency differences were found at eight of the nine loci in question and it is highly unlikely that all of these loci are linked to genes upon which selection is acting.

Another objective of this research was to assess the distribution of genetic variation in population of *D. julianalis*. Thus F_{ST} values were examined. F_{ST} values were lower when populations from each host were analyzed separately as opposed to a single analysis of all populations. This result indicates that structuring at the population level in *D. julianalis* is related to host use as opposed to geographic location, although some geographic structuring in populations on each host was evident. The greatest geographic structuring was realized in cat-tail populations (F_{ST}=0.048). Approximately half (F_{ST}=0.029 and 0.023) as much geographic structure existed in common bagworm and musk thistle populations.

Indirect estimates of migration (i.e., uncommon alleles, Nm, and correlations among allele frequencies) indicate that a reduction in gene flow exists among populations of *D. julianalis* on different host plants. First, the presence of uncommon alleles in one and/or two of the hosts, but not the other(s), strongly indicates that little migration is occurring among these populations. Analyses of estimates of Nm within and among hosts and correlations among allele

frequencies at sympatric sites indicate that populations of *D. julianalis* from musk thistle and common bagworm share more migration, than either of these hosts do with populations of *D. julianalis* from cat-tail.

Analysis of Rogers genetic similarity and Modified Rogers genetic distance, produced results similar to those of the estimates of migration. In that populations of *D. julianalis* from cat-tail are most distant and thus less similar to populations sampled from musk thistle and common bagworm. The phenogram generated by UPGMA of Modified Rogers genetic distances indicate that two distinct groups exist in *D. julianalis*, one of cat-tail populations and the other is represented by musk thistle and common bagworm populations. In the musk thistle and common bagworm group all of the populations are separated according to host except one. Waring *et al.* (1990) reported that patterns in which populations group by host and not geographic location is indicative of a shift that occurred first in one location and then moved subsequently across the range of the host. The alternative hypothesis is that shifts occurred independently across the range of the host. If this were the case then one would expect the tree to group by geographic location, regardless of the association with a particular host.

Populations of *D. julianalis* on musk thistle represent the most recently derived populations since musk thistle represents the newest available host to this moth. Because these populations share more migration with common bagworm populations and UPGMA analysis indicated that they were more closely related, then it is most likely that the musk thistle populations arose from populations

utilizing common bagworm. To determine the most ancestral host race of *D. julianalis* (cat-tail or common bagworm) a phylogenetic analysis would be necessary. A phylogenetic analysis would require the inclusion of an outgroup (e.g., closely related sister species) to determine the relationship among cat-tail and common bagworm populations. In future studies, it would be desirable to sample across the entire range of the species as well.

Other research is needed to understand the mechanisms responsible for the reduction in gene flow among populations on different hosts. Ecological separation may exist between races, which may be due to host preference and fidelity which would promote assortative mating. Allochronic separation of hosts also could produce assortative mating and could be important in this species since some temporal separation exists among hosts. Spatial separation of hosts also could introduce assortative mating, although with this moth it seems unlikely because divergence is apparent at sympatric host sites. Behavior aspects of the moth also could lead to separation, by larval conditioning (larvae tend to mate on the type of host that they were raised). Also, it would be informative to determine if any post-reproductive isolating mechanisms exist within this species. Most of these aspects could be addressed by conducting experiments on host preference and matting patterns in *D. julianalis*.

Investigations into linkage disequilibrium also would be useful. Most population genetic models of sympatric speciation predict that linkage among gene(s) responsible for habitat preference exist. These coadapted gene complexes

function to inhibit the effects of recombination. Therefore, the determination of the existence of linkage disequilibrium between loci among different hosts would be an important step to test theoretical models in natural populations.

Acknowledgment of host races in *D. julianalis* is important for future studies with this moth, especially as a biological control agent. Its role as a biological control agent of musk thistle has been examined and found to be of little importance; however, investigations as to the importance of *D. julianalis* as a biological control agent of common bagworm have not been investigated. If this organism is found to be important in controlling common bagworm, then sampling procedures should consider the host from which control organisms are collected or reared. Overall, studies such as this are important in agriculture, because we must understand what organism we are dealing with before attempts to control them can be made.

As reported earlier, few studies have attempted to observe host-associated differentiation in natural populations. The lack of studies in itself has contributed to the controversy concerning host race formation and sympatric speciation (Waring *et al.* 1990). Thus the positive results of Sturgeon and Mitton (1986), Feder, *et al.* (1988), McPheron *et al.* (1988), Waring *et al.* (1990) and this research indicate that host-associated differentiation does exist in at least some species. These studies serve as evidence for host race formation as a first step to sympatric speciation. Further research will continue to contribute to our

understanding of the intricacies of host shifts and the evolution of reproductive isloation.

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