Evolution of insect-plant relationships: chemical constraints, coadaptation, and concordance of insect/plant traits

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Abstract

Co-adaptations, co-evolution, and co-speciation between herbivores and their host plants have been topics of interest for several decades. Difficulties in deciphering these relationships as well as physiological, biochemical, and ecological adaptations of herbivorous insects themselves are discussed here in relation to biotic and abiotic environmental factors that create temporal as well as spatial mosaics of genetic variation. Hybridization was shown in swallowtail butterflies (*Papilio*) (Lepidoptera: Papilionidae) to produce some trait concordance, but mostly independent geographic trait clines (physiological, biochemical, and morphological). Strong and extensive genetic introgression of *Liriodendron tulipifera* detoxification abilities was documented northward across the hybrid zone, presumably as a result of regional climate warming only during the last 3–4 years. These and other genetic novelties produced by hybridization may be important in speciation processes, and they also emphasize the difficulties identifying appropriate taxonomic classifications for discussing any species concept. Host plant detoxification abilities (as 'key innovations') are shown capable of rapid movement between different polyphagous herbivore species independently of the host plant availability and well beyond the insect species geographical range distribution. Part of the difficulty associated with ecologically categorizing herbivore species and identifying affiliated adaptations for host plant use may be related to independent movement of various 'species-diagnostic' traits. Climate-driven local selection regimes could help generate the dynamic variation observed for co-adapted, co-evolved, or non-adapted genotypes, and may produce the confusing and changing patterns of geographic mosaics seen within and among closely related herbivores. Experimental analyses of several factors that could explain the asymmetrical shapes of trait clines across the hybrid zone for tiger swallowtail butterflies are discussed.

Introduction

Insect-plant relationships have transcended geological time and global space for hundreds of millions of years, yet have perhaps never been focused upon by humans with such intensity as in the past 30–50 years. The Symposium on Insect Plant Relationships series spans most of this period, and has monitored continual research progress toward understanding behavioral, physiological, chemical, genetic, ecological, and evolutionary mechanisms involved in these interactions. Since 1987, there have been more than 5278 scientific publications on interactions between herbivorous insects and their host plants, a nearly 3-fold increase than the previous 15 years (Scriber & Ayres, 1988). Books on the symposium topic have also increased exponentially since 1920 (numbering nearly 400; Fageria & Scriber, 2001). Virtually all of these published studies have relevance for some aspect of the evolution of insect-plant relationships.

A brief review of basic interactions should include the following categories; (1) Insect host plant recognition (and specialization), (2) Plant recognition of insects (and responses), (3) the role of Community matrices of other organisms (natural enemies, competitors, diseases) and their significant but variable

roles shaping herbivore-plant interactions, (4) Abiotic environmental factors shaping insect-plant interactions (as generators of geographic mosaics and temporal brushstrokes of the landscape ecology insects and plants perceive).

This paper is written to review some aspects of the insect-plant interactions described in this voluminous literature base. The goal was to develop an understanding for some of the fundamental difficulties we have encountered while attempting to identify general patterns found in nature and the ecological/evolutionary processes that may have created or organized them. The list of difficulties presented below ranges from the seemingly endless phytochemical ingredients (and their biochemical regulation for plant defense) and continues through various biotic and abiotic environmental factors that determine the ultimate ecological impact on individual herbivores, their population dynamics, community patterns, genetic differentiation, and speciation. The listed difficulties are not all addressed due to space and information constraints. However, a few examples from our research will be used to illustrate some of these issues. The following presentation includes the concepts of: catastrophic (extreme) environmental variance versus mean tendencies; plant defense theory; diffuse 'species' and hybridization issues; herbivore host shifts and 'key innovations' for feeding specialization; and geographical borders of species and gene flow (sometimes with 'species-diagnostic' traits moving independently of other diagnostic traits of the species). The underlying biology of each concept affects and is affected by the others, and as with the herbivores and plants, their interactions are also difficult to categorize effectively.

Difficulties identifying coevolution (at biological or chemical levels)

Specific adaptations to host plants (for habitat and food location; for adult oviposition; larval feeding, detoxification, and growth; for defense against predaceous, parasitic, or competitive enemies; for mate-finding and reproduction) may clearly be evident in certain herbivorous insects (individuals or populations). Some traits may even be characteristic enough to serve in diagnostic classification of host races, cryptic species, subspecies, or even different species of herbivorous insects (Howard & Berlocher, 1998). However, co-adaptations, co-evolution, or co-speciation between herbivores and host plants seem rarely, if ever, clearly defined or easily identifiable.

Some of the apparent reasons for this difficulty seem to include the following: (1) the existence of an extremely high diversity and temporal instability in structures and functions of particular phytochemicals; (2) limited understanding of biochemical and genetic regulation of allelochemical production and plant defense deployment; (3) natural variability in temporal and spatial distribution/abundance of herbivores; (4) significant deficits in understanding the genetic bases for behavioral and physiological adaptations of particular herbivores to plants; (5) other dynamic (and sometimes undetermined) environmental factors (host-associated biotic communities and complex abiotic variables) which shape all interactions between insects and plants; (6) difficulty determining actual selective pressures exerted by particular insects on plants, or by particular plants on insects, and any reciprocal selective interactions (co-adaptations, co-evolution); (7) difficulty recognizing the often cryptic gradations between genetic/taxonomic categories of herbivores (e.g., biotypes, host races, sub-species, and species); (8) generally unrecognized (or ignored) prevalence of geographic mosaics (local variation) and temporal flushes (in population dynamics or critical environmental conditions); (9) independent genetic segregation in geographic clines of individual traits (neutral or adaptive) for both insects and plants (intraspecifically, interspecifically, and transgenetically with GMOs); (10) a general lack of information about natural gene-flow, hybrid zone dynamics, reproductive isolating mechanisms (identifying species boundaries), and speciation processes; (11) added difficulties associated with identifying underlying mechanisms (behavioral, biochemical, physiological, ecological) for multispecies community-level interactions impacting ecosystem/biosphere energy flow and nutrient cycling functions.

The critically important combination of research approaches recommended by Stamp (1992) and Lawton (2000) requires multidisciplinary international team approaches to understand the evolution of insect-plant interactions. We have each contributed research to aid in understanding particular aspects of insect-plant interactions, many at several levels of biological organization. However, the elusive underlying organizing principals shaping patterns and processes in our world appear to be somewhat different or even unique for most (all?) species. Furthermore we have begun to realize that the variances in environmental factors are

independent of the 'average' conditions shaping biological responses. Those variances can have important and even predictable biological impacts that can not be inferred from the 'average' conditions, especially for non-linear response functions (Ruel & Ayres, 1999).

For example, intraspecific variance in host plant tissues for herbivores (Orians & Jones, 2001) may be caused by available nutrients and soil composition, microclimate, individual plant genetic differences, the plant tissue ontogeny, herbivore (or abiotic) induction responses, somatic mutations, and/or the interplay between these factors (Whitham & Slobodchikoff, 1981; Denno & McClure, 1983; Scriber, 1984a,b; Tallamy & Raupp, 1991; Städler, 1992; Karban & Baldwin, 1997). Insects may respond by choosing different feeding sites, by altering their consumption rates or by induction of physiological/detoxification enzymes (Scriber & Slansky, 1981; Bernays & Chapman, 1994). On any particular plant species, local specialization or population 'demes' may develop in sympatric herbivores (Edmunds & Alstad, 1981; Mopper, 1996; Mopper & Strauss, 1998). Analogous local specialization in generalized species of herbivores may result in a geographic mosaic of regional (allopatric) host plant species preferences (Fox & Morrow, 1981; Scriber, 1986; Thompson, 1995). Survival, population growth and community dynamics are non-linear functions affected by variance in underlying environmental conditions. Knowledge of frequency distributions and the variance of environmental driving variables can be used to give mathematical estimates of these and many other biological consequences (Ruel & Ayres, 1999).

Environmental extremes (peak variances or catastrophic 'disturbances') may be sporadic, but still have major long-term selective impacts

Despite the short measurement intervals of our research studies and the general search for organizing patterns and central (mean) tendencies, the impacts of natural selection may depend on the time and frequency of extreme environmental variations. For example, the 20–30 year averages of latitudinal trends in the seasonal 'average' degree-day accumulations was fundamental in developing the general 'voltinism-suitability' hypothesis of host plant selection across extensive geographic areas of North America (Scriber & Lederhouse, 1992). However, the unpredictability of the second coldest year on record for Michigan in 1992, had drastic impacts on species distribu-

tion limits. Following several warm years northward range extensions and the second warmest year (1991) on record to that date, the severe cool season of 1992 extirpated essentially all populations along the northern geographic distribution of *Papilio cresphontes*. The second generation of these primarily subtropical Rutaceae-specialists grew particularly slowly and failed to complete pupation before the first severe fall freeze killed essentially every individual in the State from 43.5 to 41.5 deg North latitudes. Most of the casualties were early to mid-larval instars, but even final instar larvae were frozen solid while clutching leaf petioles (Scriber & Gage, 1995).

Similarly, the extremely limited distribution of freeze-free days in the climatic 'cold pockets' of northern Michigan (less than 70 days between last spring and first fall freezes; 50–year average 1930–1979) apparently selected for small female pupal size in *Papilio canadensis* (Scriber, 1994) as in Alaska (Ayres & Scriber, 1994). In addition, we observed unique local feeding preferences by these particular *Papilio canadensis* for the most nutritious local host plant species (*Fraxinus americana*), which exhibits delayed bud break and slow leaf maturation relative to the adjacent birch, aspens, poplars, cherries, and basswood host plant species (Scriber, 1996a). However the recent few years (1996–2000) have been much warmer than average, with 1998 the warmest year on record (Hughes, 2000), which has significantly affected the gene flow and trait cline patterns of these swallowtail butterflies across these colder areas of northern Michigan. These previously detectable geographic behavioral mosaics in local *P. canadensis* host preferences (shaped by local climatic cold pocket selective pressures during the 1980s and early 1990s) may have largely disappeared with the significant recent regional warming in northern Michigan (Giroux, 1998; Scriber, 2002b). It has been hypothesized that such thermal constraints from late spring and early fall freezes may be responsible for maintaining high frequencies of hybrid (introgressed) genotypes in giant silkmoths of the *Hyalophora cecropia* species group in California. This area of hybrid *Hyalophora* may be the result of differential survival in late larval instars since hybrids develop faster and pupate sooner than parental types by several days, avoiding the sporadic but serious early winter killing freezes (Collins, 1984). This phenomenon could also serve as a potential explanation for some of the stable levels of interspecific *Papilio* introgression in the Great Lakes island pop-
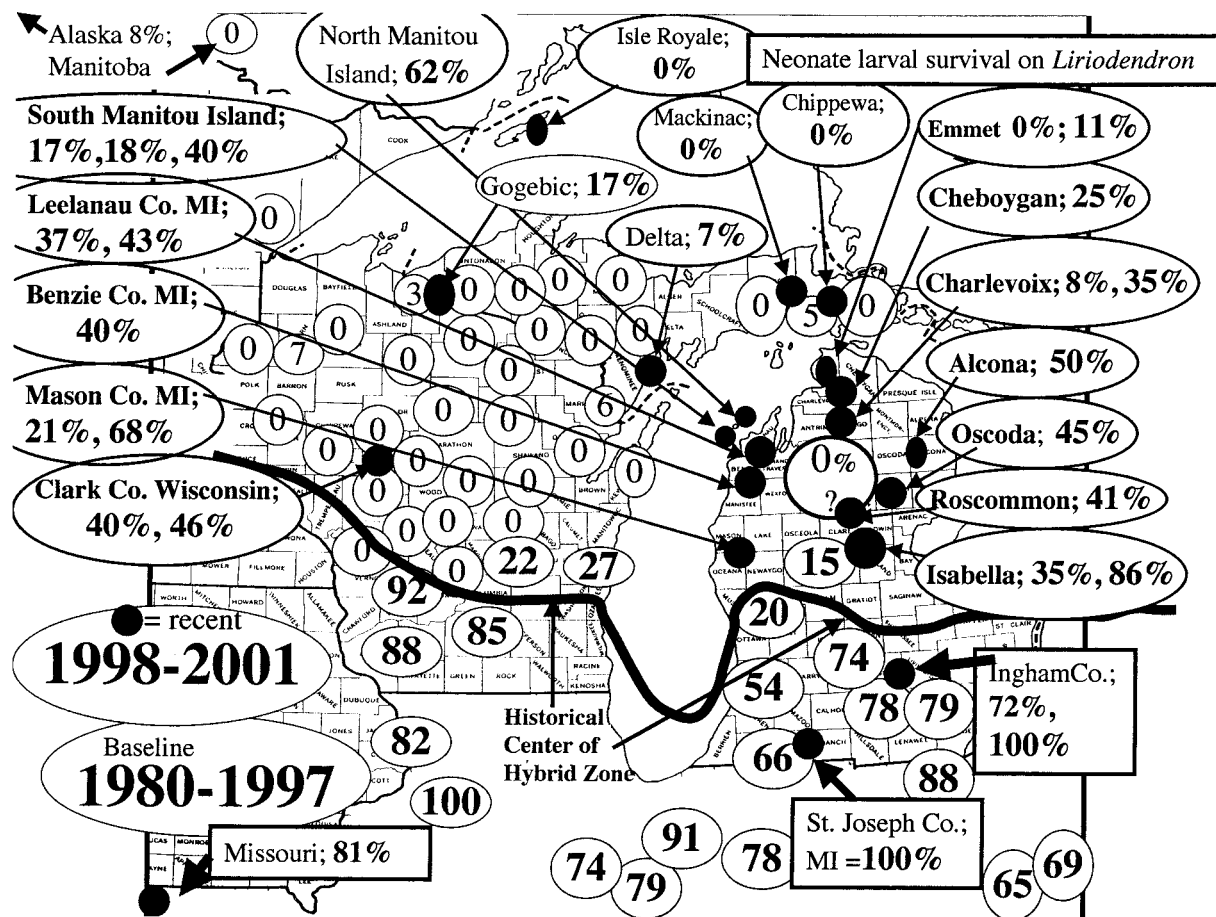
Figure 1. The neonate (first instar) larval survival of tiger swallowtail butterfly populations around Michigan and Wisconsin in no-choice studies on tulip tree leaves, *Liriodendron tulipifera*. The heavy line represents the northern limits of tulip tree distribution (Scriber, 1983) and the historical center of the hybrid zone during the 1980's and early 1990's. The differential survival (percentage of the initial total number of neonates surviving to the second instar) of *P. glaucus* (in the south) and *P. canadensis* (in the north) is delineated by population location in the circles. Results of recent bioassays from 1998–2001 (1637 larvae from 136 families) are indicated by county with ovals for *P. canadensis* and rectangles for *P. glaucus* populations. Single values indicate that the percentages were lumped over several years (prior to 1998). Two or three values represent the percentages in two or three different years (during the 1998-2001 period). In these recent four years it is clear that the traits conveying detoxification of tulip tree phytochemicals have moved northward extensively in *Papilio* of Wisconsin and Michigan, even though the host plant has not.

ulations (Ording, 2001) or near the Michigan cold pockets (Scriber, 1996a).

It also appears that extensive genetic introgression has occurred from the more southern *P. glaucus* swallowtail species during these extremely warm years (1998 and 1999). These regional climate changes appear to be altering the suite of 'diagnostic' population traits of the *P. canadensis* populations with an asymmetrical introgression northward across the hybrid zone (from Wisconsin in the West, throughout Michigan and New York to Vermont and Massachusetts in the East; Ording, 2001; Scriber, 2002b). This recent interspecific hybrid introgression includes

morphological, behavioral, physiological detoxification, diapause, and molecular traits (see below). It has been suggested that dynamic oscillations in host range, rather than continued specialization, may drive the diversification of plant-feeding insects (Janz et al., 2001). Hybridization may play a large role in generating genetic diversity for selection to act upon (Arnold, 1997). For example, the autosomally controlled tulip tree detoxification abilities have shifted extensively northward in many tiger swallowtail populations across the *P. glaucus-canadensis* hybrid zone (WI, MI, NY, and VT) in the past 3-4 years, even though the host plant has not (Figure 1). This type

of genetic introgression of physiological traits has not been observed for aspen detoxification abilities southward of the hybrid zone center (Figure 2).

The extremely rapid genetic divergence (and even speciation) that can occur with invasion of new habitats has been documented for several biological systems recently (Schluter, 1996, 1998; Carroll et al., 1997; Losos et al., 1997; Orr & Smith, 1998; Rieseberg & Burke, 2001). The potential power of regional climatic warming to spread genetically-based traits throughout the species (or into other species) over extensive geographic areas seems evident in our observations of tulip tree detoxification abilities and morphometric wing pattern traits in the Great Lakes region, New York, and New England (Figures 1–5). The latitudinal and altitudinal movement with several years of climatic warming 'legacies' of bivoltine life histories from univoltine populations is also evident in these *Papilio* species (Scriber & Gage, 1995) as well as other Lepidoptera, including pest species such as the European corn borer (Scriber & Lederhouse, 1992). It is also feasible that other pest shifts from semi-voltine to univoltine may open up a 'waterfall effect' where larger populations of serious pests such as mountain pine beetles could spill across much of a region, or even most of North America, due to continued global warming. Such warming will eventually exceed the lower levels resulting in non-functional 'fractional voltinism' partial generation changes to higher threshold levels (as occurred in the 1930s) permitting functional voltinism shifts and 'climatic release' of populations (Logan & Powell, 2001). These functionally 'new' ecological habitats may be involved in many of the successful insect invasions of North America (Niemelä & Mattson, 1996).

How do insect-plant interactions evolve; and when is it coevolution?

The concept of reciprocally-induced evolutionary changes between plants and insects was introduced using examples of plants that appeared chemically defended in a similar fashion and insects that had overcome these defenses over long periods of evolutionary time. Such examples suggest existence of a 'coevolutionary' interaction between insects and plants, identifiable at general family-levels allowing a general congruence in phylogenetic trees of insects and plants to be discerned (Ehrlich & Raven, 1964; Berenbaum, 1983; Mitter et al., 1988; Farrell

et al., 1992). Sometimes insect host plant specializations may even serve to clarify plant systematics (Dethier, 1941; Abrahamson et al., 1998). Since the cause and effect mechanisms underlying these putative reciprocal responses have been difficult to identify with any certainty, the concept of coevolution (Janzen, 1980) has been challenged and modified to include less strict variations of the theme, including: 'diffuse coevolution' (Fox, 1988), 'geographic mosaics of coevolution' (Thompson, 1994), and 'sequential evolution/colonization' (Jermy, 1976, 1984; Mitter & Brooks, 1983). It seems that sequential evolution provides the most credible academic following. However, specialization is not necessarily an 'evolutionary dead end' (Menken, 1996; Thompson et al., 1997; Schoonhoven et al., 1998; Janz et al., 2001; Teotonio & Rose, 2001). In fact, phenotypic plasticity may itself be adaptive, leading to genetic differentiation and speciation in novel habitats or under different environmental conditions (Agrawal, 2001).

Do herbivores serve as selective agents on plant defenses?

Plant chemistry certainly impacts herbivores and provides a fundamental basis for resistance. However, studies to test coevolutionary theory have thus far failed to provide direct evidence of insects as selective agents for phytochemical defenses (Thompson, 1994; Price, 1997; Schoonhoven et al., 1998). Plant defenses lost as the result of genetic drift in the absence of selection, or situations where secondary chemicals aid in adapting to the physical (abiotic) environment, the role of 'balance' and 'availability' of soil nutrients, and the more direct/detectable genetic and biochemical responses of plants to pathogens, warrant considerable attention and additional study.

The diversity and redundancy of chemical structures or functions (Romeo et al., 1996; Ayres et al., 1997) and the phytochemical induction by other herbivores or the abiotic environment (Tallamy & Raupp, 1991; Karban & Baldwin, 1997; Agrawal et al., 1999; Tollrian & Harvell, 1999) complicates identification of 'key innovations' that might be involved in a lineage of herbivores that has broken a barrier in the presumed 'chemical arms race' between insects and plants (Berenbaum, 1983; Berenbaum et al., 1996). Phytochemical induction impacts of *Populus* hybrids were difficult to detect using six 'Salicaceae-adapted' insect species (Parry, 2000; but see Lindroth
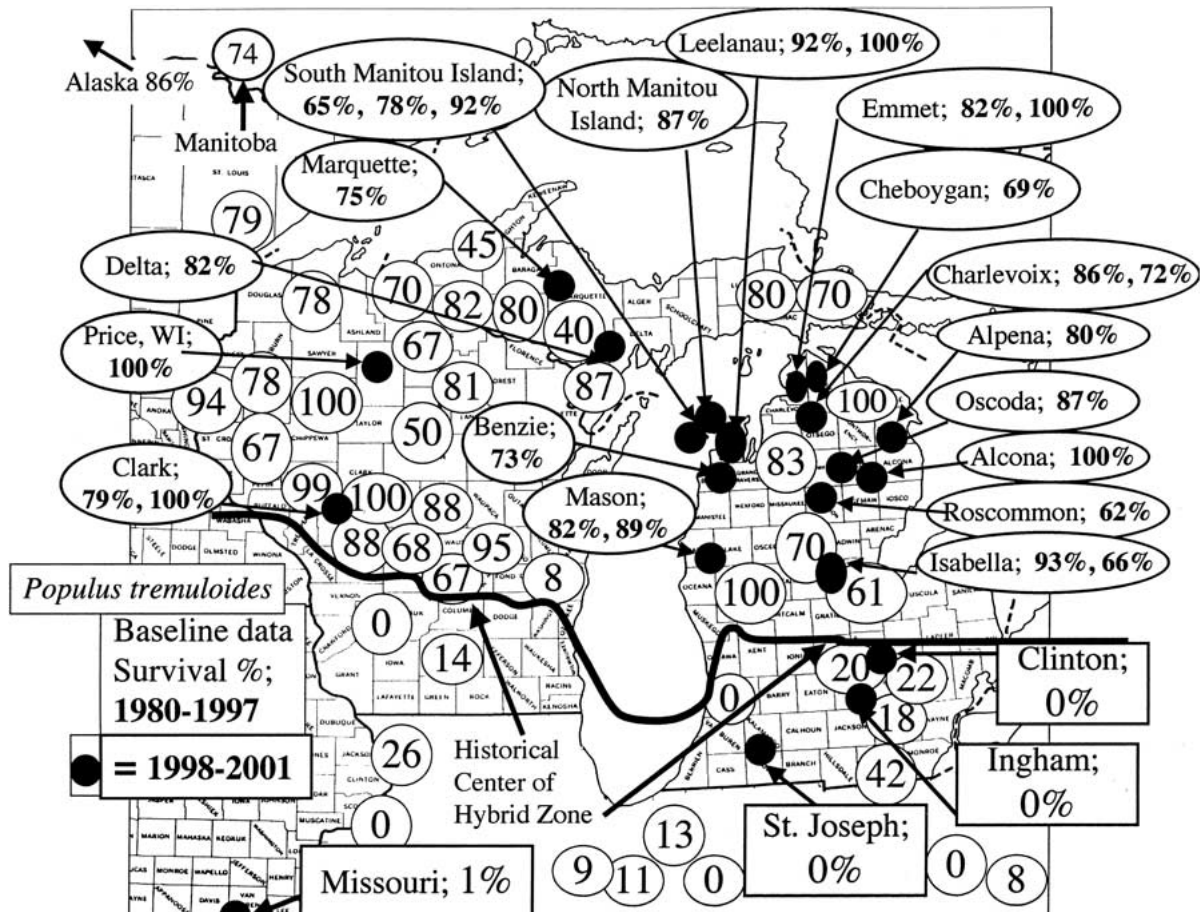
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Figure 2. The neonate larval survival of *Papilio* populations in no-choice feeding bioassays using quaking aspen (*Populus tremuloides*) leaves. As indicated in Figure 1, the center of the hybrid zone (*P. canadensis* to the North and *P. glaucus* to the South) is indicated by the heavy line, and the numbers in small circles represent multi-year county survival averages of all first instar larvae tested on aspen. The larger ovals represent the recent four years (1998–2001), with multiple percentages indicated for each yearly average when multiple-year bioassays were possible for a given county site (indicated by dark symbol at end of arrows). The totals for the last four years are 1453 larvae from 134 families, with many more families and individuals in 1980–1997. A few quaking aspen trees occur in patches south of the hybrid zone/ecotone line, but generally they decrease rapidly to none at the southernmost locations shown here (northern Illinois and Indiana; Scriber, 1983). In contrast to northward movement of tulip tree detoxification abilities (Figure 1), the traits conveying aspen detoxification abilities have not moved beyond the hybrid zone center (southward) during recent years. Offspring from Clinton, Ingham, and St. Joseph counties in Michigan show no ability to survive on aspen during the past 4 years.

& Hwang, 1996) or 'unadapted' insects (that all avoid or die eating it; Scriber et al., 1989, 1999). However, using a continuum of genotypic variants created with experimental hybridization and backcrossing of closely related *Papilio* species (one Salicaceae-adapted and one not) permitted us to detect subtle, yet real induced changes in experimental gypsy moth defoliated (and unfertilized) trees compared to defoliated fertilized and undefoliated fertilized/unfertilized combinations (Scriber et al., 1999).

Environmental 'stress' can greatly influence plant susceptibility to herbivores and pathogens (Mattson &

Haack, 1987; Waring & Cobb, 1992; Koricheva et al., 1998). The time subsequent to the stress may be an undervalued aspect of such relationships (Wallin & Raffa, 2001). Tolerance of insect herbivores by plants has often been presumed to be enhanced by fertilization, however results are equivocal (Scriber, 1984b; Mattson & Scriber, 1987; Herms & Mattson, 1992; Strauss & Agrawal, 1999; Stowe et al., 2000). A meta-analysis of plant responses to herbivory shows fundamental differences between monocots and dicot herbaceous and woody plants, perhaps explaining
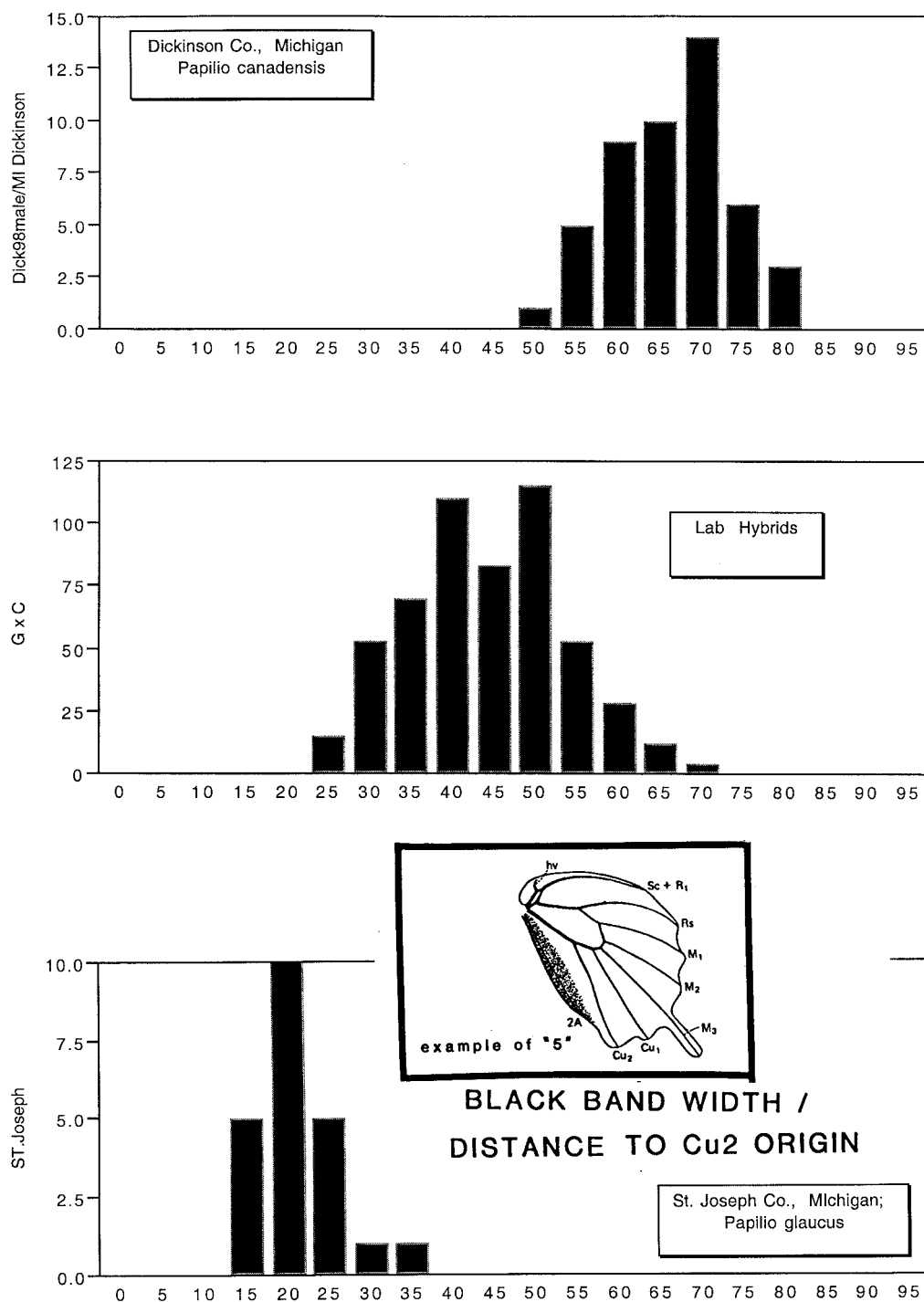
Figure 3. Frequency plots for species-diagnostic hindwing (relative black band width) traits of *Papilio* individuals from the Upper Peninsula, Dickinson Co. MI (*P. canadensis*; mean 67.0%, $n = 448$), from southwestern Michigan St. Joseph Co. (*P. glaucus*; mean 23.2%, $n = 35$, compared with several hundred offspring of 29 different primary hybrid families (*P. glaucus* females × *P. canadensis* males; a similar pattern was seen for the reciprocal type of crosses, not shown). An example of 50% 'hybrid-type' black band width in the hind wing is inserted. *Papilio glaucus* males typically have relative black band widths of 10–40%, while *P. canadensis* typically have 55–90%.
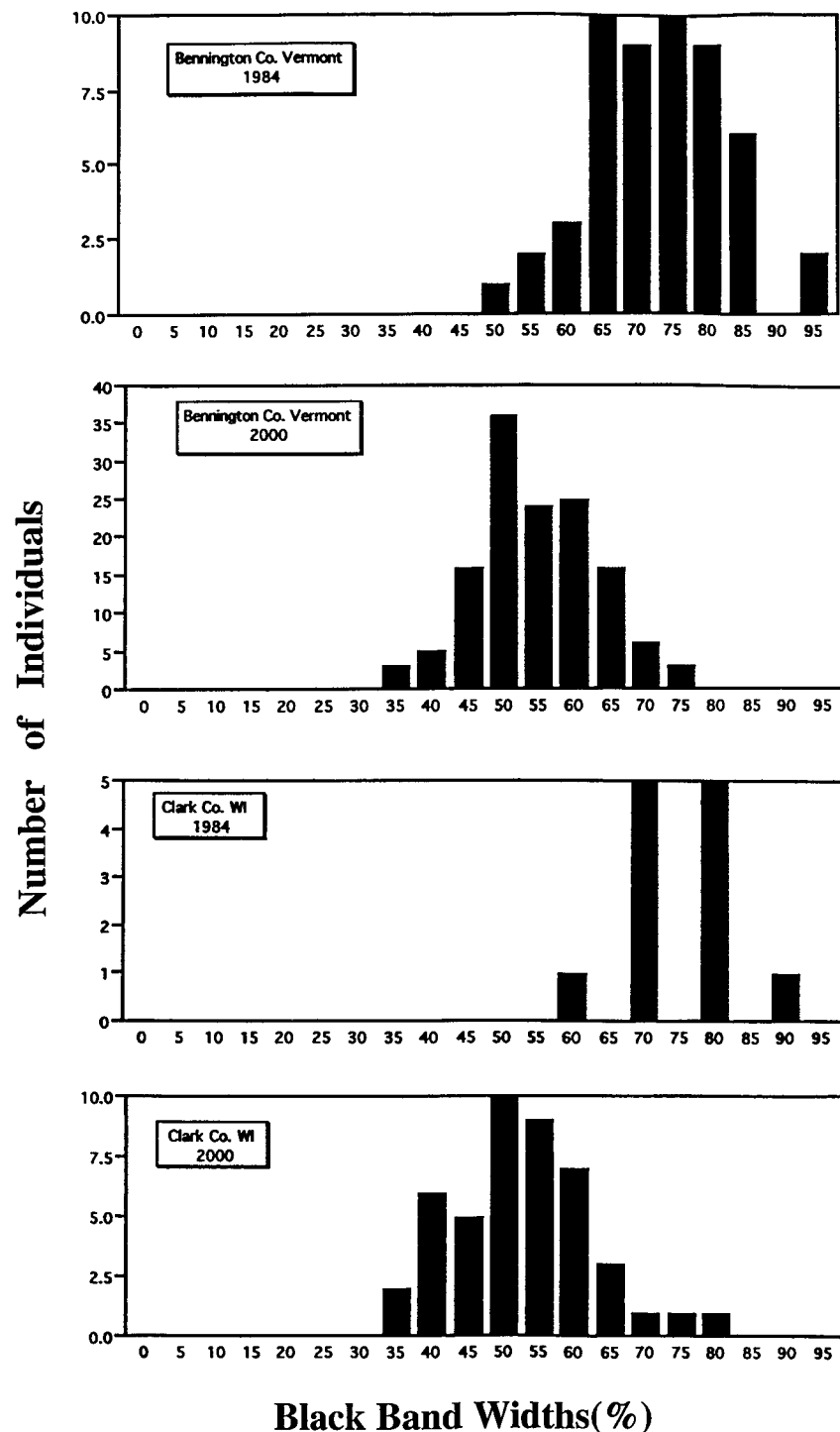
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Figure 4. Frequency plots of hindwing traits (relative black band widths) for individuals of two widely separated populations (Clark Co. Wisconsin; and Bennington Co. Vermont) that are each near the center of the hybrid zone between *P. canadensis* and *P. glaucus*. The most recent dates sampled (1998–2001) show patterns of band-widths that are becoming narrower, or less '*canadensis*-like', reflecting morphological evidence of genetic introgression in these areas. For example, in 1984 males from Bennington Co. in Vermont had a mean of 72.0%; $n = 50$ and in 2000 had a mean of 54.6%; $n = 134$; with t-test showing significance at $P < 0.00001$); in 1980–1984 male tiger swallowtails in Clark Co. Wisconsin had a mean of 75.0%; $n = 12$ and in 2000 had a mean of 52.7%; $n = 45$ which is also significantly different (t-test, $P < 0.00001$).

the contradictory results in the literature (Hawkes & Sullivan, 2001).

A nice review of plant defense theory and a series of non-mutually-exclusive hypotheses/theories is presented by Herms & Mattson (1992) and Price (1997). These include: (1) Climatic release hypothesis; (2) Plant Stress; (3) Plant Apparency; (4) Induced defense hypotheses; (5) Carbon-nutrient Balance; (6) Resource Availability; (7) Plant Vigor and 'Biological Stoichiometry' (Elsner et al., 2000); (8) Voltinism-suitability hypothesis (Scriber & Lederhouse 1992), (9) Plant-plant or plant-enemies communications ('S.O.S.'; Bruin et al., 1995; Turlings et al., 1995; Dicke, 1999), among others.

Evidence that natural selection on diet breadth of insect herbivores may be strongly influenced by associated natural enemies (Atsatt & O'Dowd, 1976; Bernays & Graham, 1988; Dyer, 1995; Camara, 1997) and directly, or indirectly, by competitors (Denno et al., 1995; Dankert et al., 1997; Redman & Scriber, 2000) also complicates detection of diffuse coevolutionary interactions. Plant parasites have been shown to affect both the cyanogenic and acyanogenic *Trifolium repens* and differentially affected the associated invertebrate herbivores (Puustinen & Mutikainen, 2001). In addition, there is a critical need to simultaneously consider the interaction of herbivores and pollinators on alkaloids, other chemicals, and plant fitness traits (Adler et al., 2001). Local deme formation shows that highly dispersive insects can show greater local adaptation than sessile insects (i.e., dispersal ability is a poor predictor of genetic isolation, especially for endophagous leaf-miners and gallers; Mopper, 1996). Such variables make it difficult to assess relative importance of 'top down' and 'bottom up' pressures on population dynamics and genetic divergence (Price, 1997).

A review of the literature for insect tri-trophic/community interactions from both fundamental and applied aspects concludes that several factors preclude a synthesis of the relative roles of top-down or bottom-up forces (Walker & Jones, 2001). Furthermore, the community patterns of dozens of arthropod herbivores were shown to be significantly influenced by aphids, predatory ants, plant quality, and plant hybrids (Wimp & Whitham, 2001). Interactions between insects and host plants, some putatively coevolutionary, will always be mediated to variable degrees by the ever-changing biotic and abiotic community (Strong et al., 1984) as well as ecological opportunities and constraints imposed by plant defensive chemistry (Feeny, 1995).

Intraspecific spatial 'mosaics' in plant chemistry and insect genotypes

The degree to which a 'key innovation' such as furanocoumarin detoxification (Berenbaum et al., 1996; Hung et al., 1996) in a herbivore lineage allows the successful establishment onto a new adaptive regime of previously 'resistant' plant chemistry depends upon the variability in the selection regime of the plant and the genetically-based variability in the behavior, physiology, and ecology of the herbivore (Scriber et al., 1991; Fritz & Simms, 1992; Coley & Barone, 1996; Caterino & Sperling, 1999). Geographic mosaics of local specialization in insect behavior (Gould, 1991; Bernays & Chapman, 1994; Bernays, 1998), detoxification physiology (Nitao et al., 1991; Hoy et al., 1998), and other insect genetic adaptations (Thompson, 1994; Mopper & Strauss, 1998) seem likely in most communities. However, these specialized herbivore traits are poorly known in relation to the underlying geographic variation in plant phytochemistry or palatability (Rausher, 1992; Johnson & Scriber, 1994; Pennings et al., 2001).

Local patchiness in foliar concentrations of a single toxin can create habitat patchiness in *Eucalyptus* for marsupial folivores (Lawler et al., 2000). Four species of herbivorous Lepidoptera all feeding on the same species (*Lotus corniculatus*) in a patchy environment, all spatially segregated independently into their own metapopulations which would suggest 'diffuse' adaptation mechanisms (Gutierrez et al., 2001). Temporal considerations and different spatial scales have led to attempts to link geneologies and geography, in an academic field called 'phylogeography' (Avise, 2000). Differences in plant chemicals and level of browsing from Alaska to Finland suggest that defensive plant chemistry may be influenced by herbivores across large biogeographic areas (Bryant et al., 1989) perhaps extending millions of years for Magnoliaceae in China and the USA (Sewell et al., 1996). These plant-herbivore relationships become even more interesting and complicated with more localized plant hybrid zones.

Plant hybrid zones and insect hybrids (sources of genetic variation or taxonomic confusion?)

The first problem facing an ecologist interested in a particular insect-plant interaction is identifying the species of each. The basic processes of speciation in herbivorous insects are poorly understood, despite decades of analyses and debates (Howard & Berlocher, 1998). It has been estimated that Angiosperm plant speciation has involved polyploid hybrids in a large proportion (30–70%) of all species (Grant, 1981; Whitham et al., 1991; Arnold, 1997). Endler (1998) defined hybrid zones as: 'places where two or more populations of individuals are distinguishable on the basis of one or more heritable characters, overlap spatially and temporally, and cross to form viable and at least partially fertile offspring'; and introgression as 'the movement of genes or alleles from one population or species into another'.

Most species concepts are built upon the belief that hybridization and hybrids are 'bad' (Rhymer & Simberloff, 1996) or unlikely to be of significance because of several poor concepts described by Arnold (1997). For example, (1) 'good' species do not hybridize because they are defined as not interbreeding; (2) unfit hybrids will ruin the purity of parental types; (3) hybrid progeny are 'always' less fit evolutionary dead ends; or (4) hybridization violates the laws of cladistic analysis. Arnold describes how the common 'species concepts' often prevent consideration of hybrids and hybridization as sources of new adaptations to the environment. For example, the 'biological species concept' identifies species by the (purported) fact that they do not interbreed, so hybrids are discarded as early stages of divergence, 'aborted speciation', or accidents. Similarly, the 'phylogenetic species concept' defines species as basal clusters of organisms, recognizably different from other such clusters, and within which there is a paternal pattern of ancestry and descent, determined from branching patterns in the cladogram (which by definition does not include reticulate patterns caused by hybridization; see also Endler, 1998).

At least three types of hybrid zone models have been advanced (see also Harrison, 1993); (1) the 'Tension Zone' model with selection against hybrids in the hybrid zone with gene flow from the parental zones; (2) the 'Mosaic' model with different habitat patches across the center of the hybrid zone; (3) the 'Bounded Hybrid Superiority' model with a central zone where hybrids are more fit and marginal areas where parental

types are more fit, with gene flow among them. Hybrids may actually be superior to either parent in some circumstances (i.e., new adaptive forms), depending upon local microhabitats, host plant, and the particular year in which fitness is measured (Collins, 1984; Arnold & Hodges, 1995; Porter et al., 1997; Scriber et al., 2002a).

A positive correlation between heterozygosity at allozyme loci and fitness components such as growth, survival, fecundity, oxygen consumption, mating success, and developmental stability has been reported for meta-analyses of populations of many species (Watt, 1994; Britten, 1996; David, 1998). This leads to Arnold's (1997) 'Evolutionary novelty' model of hybrid zones (see also Smith et al., 1997). In this model, if hybrids become established in new habitats, they can become a new subspecies/species (cladogenesis), spread out, and replace one or both of the inferior parental types. The outcome depends on which hybrid genotypes are formed, the local microenvironmental interactions, and natural selection observed across the region. At species borders and hybrid zones, ecological and genetic analyses of differentiation and reproductive isolation can be studied most effectively (Sperling, 1990; Jiggins & Mallet, 2000).

We unfortunately know little about the fitness heterogeneity in relation to that of the habitat, such as insect herbivores in relation to 'mosaic' versus 'gradient' type hybrid zones (Endler, 1998). We also need more precise measurements of barriers to (Rieseberg et al., 1999) and mechanisms affecting hybridization (pre-zygotic and post-zygotic). We need to be able to detect and understand rare events (e.g., 'key innovations') that may give rise to an exceptionally high diversity of insect-plant interactions (Berenbaum et al., 1996) and how adaptation itself can lead to speciation (Schluter, 1996, 1998; Bradshaw et al., 1995; Caillaud & Via, 2000). We need to better understand the role of 'gene flow' in spreading advantageous alleles among geographically separated populations (in like environments) as well as local restriction of gene flow in other (local) environments (Thompson, 1994; Mopper, 1996; Bossart, 1998; Rieseberg & Burke, 2001).

If geographic distance was the only factor considered in gene flow models between populations (MacArthur & Wilson, 1967) or metapopulations (hybridizing or otherwise), we risk missing the more critical barriers to gene flow. For example, the intervening habitat quality will determine the 'effective distance' or ecological barrier strength (Porter et al.,

1997; Moilanen & Hanski, 1998; Roland et al., 2000). Our own analysis of interspecific hybridization of *Papilio glaucus* and *P. canadensis* has shown that thermal units are resources themselves, affecting the quality of the 'habitat' for growth and reproduction (thereby locally selecting for certain host plant species of the highest nutritional quality; Scriber, 1996a). Recent surveys of species and hybrid 'diagnostic' morphological traits illustrate that trait clines are more precisely predicted by thermal unit accumulations (degree days) than by latitude or geographic distance, especially in mountainous areas with long steep river valleys as in New York State, Pennsylvania, and New England (Scriber, 2002b). These qualitative differences in intervening habitat quality, phytochemistry, and other environmental resources are also temporally variable, affecting the preference-performance relationships of herbivores (Cronin et al., 2001). Plant and animal parasites often find hybrid hosts more susceptible than parental types, but other patterns can be shaped by genotype/environment interactions (Fritz, 1999; Moulia, 1999).

Specialization in herbivore-plant interactions and 'trade-offs'

The direction of specialization among insect-host plant interactions is reviewed by Janz et al. (2001). Basically, the patterns emerging from studies of the evolutionary dynamics of host-plant specialization show: (1) a strong predominance of specialists in many taxa (e.g., Papilionidae, Scriber 1983, 1984c; Saturniidae, Janzen, 1988); (2) strong taxonomic conservatism in host plant utilization patterns (Ehrlich & Raven, 1964; Berenbaum 1983; Fiedler, 1996; Janz & Nylin, 1998); (3) Phylogenetic congruence (co-speciation; parallel cladogenesis) is rare in insect plant interactions (Menken, 1996); (4) Processes involved in host shifts/specialization have become the focus of recent work, rather than co-evolution or co-speciation (Scriber et al., 1995; Janz & Nylin, 1998; Boggs et al., 2002)

Host races and speciation

Sympatric origins of host races have been described with increased frequency (Bush, 1969, 1994; Craig et al., 1997; Howard & Berlocher, 1998; Caillaud & Via et al., 2000; Via, 2001, and references therein).

Evolution of genetic differences associated with host plant utilization (or other traits) between populations can be greatly accelerated in those that colonize novel environments or new habitats (Carroll & Boyd, 1992; Fox et al., 1997; Losos et al., 1997; Orr & Smith, 1998). Novel selection pressures rather than drift appear to promote reproductive isolation and rapid speciation in some species, with speciation rates doubling on islands (even small ones) and at even greater rates in lakes (Schluter, 1998).

Preference-performance correlations have been observed for three races of *Eurosta solidaginis* (Tephritidae) and allochronic isolation seems to have resulted in reproductive isolation (Horner et al., 1999). In *Rhagoletis pomonella* and other hawthorn-infesting flies (also Tephritidae), it has been the developmental timing and diapause of the pupae (adapting to fruiting phenology) rather than any host-associated fitness trade-offs in larval specialization that appears to be most important in this divergence (Feder, 1998).

Loss of ability to use ancestral hosts with increased specialization (Jack-of-all-trades, master-of-none concept) has had variable results at the physiological efficiency level (Scriber & Feeny, 1979; Carroll & Boyd, 1992; Thompson, 1996; Scriber, 1996b; Bernays, 1998; Agrawal, 2000; Singer, 2001, and references therein). However, physiological efficiencies are only one of many potentially important trade-offs in life history traits. Different population and environmental 'mosaics' make it difficult to determine the genotypes of herbivores and the critical phytochemistry of plant species/ genotypes (or genetically modified transgenics). Also it is difficult to separate genetic trade-offs (antagonistic pleiotropy) from 'drift decay' (or mutational accumulation; Futuyma & Moreno, 1988). However, 20,000 generations of experimental selection with bacteria have shown that antagonistic pleiotropy rather than drift decay is the most likely explanation for thermal specialists having reduced performance at other temperatures (Cooper et al., 2001) and why resource specialists (fed glucose) improve by specialization (Cooper & Lenski, 2000).

Regardless of host specialization trade-offs, there are interesting similarities in the temporal isolation of *Rhagoletis pomonella* host races in pupal diapause and adult emergences across the Great Lakes region with the voltinism and species differences maintained between the Canadian and Eastern Tiger Swallowtail butterfly species (*P. canadensis* and *P. glaucus*, respectively). Also, allochronic isolation rather than only host-associated reproduction seems to be critical

in three host races of Tephritids on goldenrod (Craig et al., 2001). As with the apple flies, *P. glaucus* is a facultative diapauser, with multiple generations in latitudes with sufficient degree-day accumulations or 'thermal time'. The Canadian swallowtail does not respond to photoperiod cues and appears to be a univoltine 'obligate' diapauser everywhere from Alaska into Wisconsin, Michigan, and New England. These differences in tiger swallowtails are controlled by X-linked factors (females are heterogametic). Pupal diapause prevents direct adult development (a second flight) in all *P. canadensis*, which means that May and June are the only time for them to mate and reproduce. While the majority of *P. glaucus* adults directly develop and emerge for a second generation across 99% of their geographic range, those at higher latitudes nearer the hybrid zone appear to 'bet hedge' with a significant proportion diapausing in the first generation. Second flights in a season have not been observed anywhere for *P. canadensis*.

A 'false second' July generation seen in the NY/VT population with high introgressed allele frequencies of both *P. glaucus* and *P. canadensis* (and heterozygous) types supports the idea that different pupal emergence rates (*P. canadensis*, early; *P. glaucus*, late; hybrids intermediate) may be a significant reproductive isolating mechanism, near the areas with 2500 degree days of seasonal heat accumulations (Scriber et al., 2002b). Since a 'true second generation' requires 2600–2800 F degree days it is likely that 'fractional voltinism' (with mortality of those failed attempts at a second generation exists in these areas of NY/VT; Scriber, 2002b). Morphological evidence from wing band patterns (Figures 3–5) and diagnostic allozymes (Pgd-100 and Hk-100; Ording 2001; Scriber, 2002b) strongly suggest this geographically-widespread interspecific hybridization (northward movement of 'glaucus-like' traits) is a recent happening, perhaps enhanced by regional climate warming from 1998-present (Parmesan et al., 1999; Hughes, 2000; Scriber, 2002b).

Barriers to interspecific gene flow appear to be minimal in this *Papilio* hybrid zone region. It has been shown experimentally that interspecific field mating preferences are asymmetrical for *canadensis* males and *glaucus* males and as such, do not significantly help maintain pre-zygotic isolation in central and northern Michigan (Deering & Scriber, 2002). Females and males of both species are multiple-maters, but there is no consistent pattern of sperm precedence or 'cryptic sexual selection' of conspecific sperm post-mating (Eberhard, 1996; Stump, 2000). Post-zygotic reproductive isolation is also not effective at preventing successful hybridization between the two tiger swallowtail species (Donovan, 2001; Scriber et al., 2002a).

Information from 'key innovations' and long term *Papilio* studies

Use of Rutaceae by the ancestral prototype of all six species of the polyphagous North American *Papilio glaucus* group is a likely carryover from a 'key innovation' involving several major sections of the 200 species genus *Papilio* (Berenbaum et al., 1996; Hung et al., 1996; Li et al., 2000). Detoxification mechanisms such as the cytochrome P450 monooxygenases used in detoxifying furanocoumarins of the Apiaceae and Rutaceae may play central roles in determining: (1) the strong preponderance of specialists, (2) strong taxonomic conservatism in host affiliations, and (3) why specialization is not a dead end (Janz et al., 2001). Perhaps these gene families can metabolize a wider range of toxins in related families eaten by generalized *Papilio* species (e.g., *P. glaucus* and *P. canadensis)* such as Betulaceae, Magnoliaceae, and Rosaceae, as well as Rutaceae (Berenbaum & Zangerl, 1998). For example, *P. glaucus* larvae can eat more than 120 species in 34 families (Scriber, 1988). Local adaptations of *P. glaucus* may be mediated by different gene families of P450's (Nitao, 1995; Hung et al., 1996). This generalist also makes more oviposition errors than more specialized congenerics (Scriber et al., 2001a) as is the case with other Lepidoptera species (Nylin et al., 2000).

Differential use of tulip tree, *L. tulipifera* and quaking aspen *P. tremuloides* has been the focus of our long term analyses since 1980. The geographical ranges of tulip tree and aspen overlap near the ecotone between boreal forests (aspen-birch) and temperate deciduous forests throughout the Great Lakes region. Despite the fact that these tree distributions have essentially remained constant over the past two decades, we have recently seen extensive northward flushes of tulip tree detoxification abilities into what were previously 'pure' *P. canadensis* populations (which lacked larval abilities to feed on this species; Scriber, 1982). The genetic basis of inheritance in both quaking aspen and tulip tree detoxification abilities has been determined to be autosomally controlled, appearing in both sexes of reciprocal hybrids (Scriber, 1986).
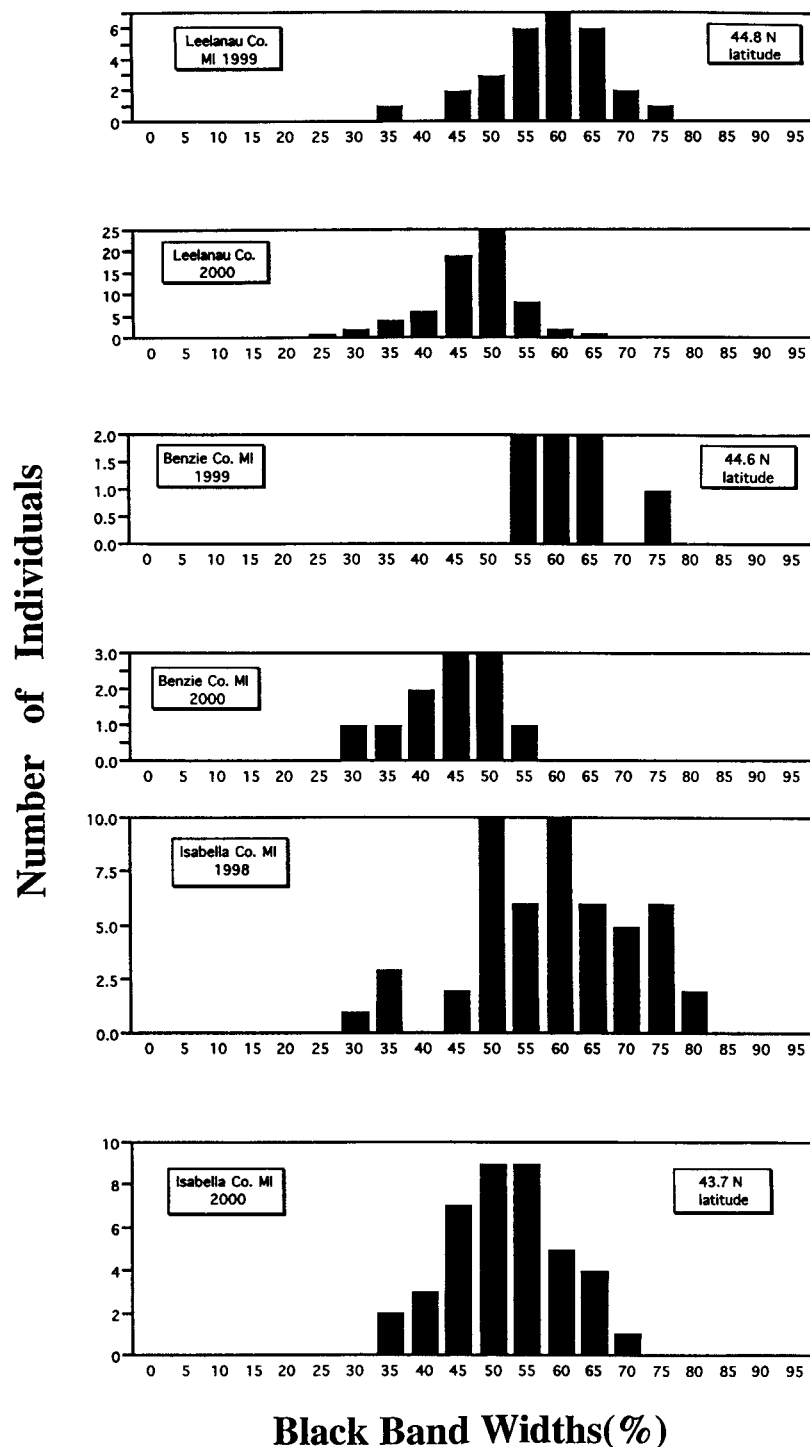
Figure 5. Frequency plots showing changes in the average hindwing traits for individuals in three counties of central and west-cantral Michigan. In Leelanau Co. 1999 mean 60.1; $n = 29$ while the mean was 47.0; $n = 68$ and significantly less in 2000 (t-test, $P < 0.001$). Just slightly to the south in Benzie Co. the 2000 mean (44.0; $n = 7$) was also less $P < 0.001$ than in 1999 (62.1; $n = 11$). In central Michigan northern Isabella Co. (near border with Clare Co.) the mean was also significantly less (t-test; $P < 0.006$) in 2000 (52.4; $n = 34$) than in 1998 (58.9; $n = 50$).

Backcrossing of hybrids with parental types is easily accomplished in the lab (and apparently in the field), and these detoxification traits appear quantitative in nature, but controlled by relatively few genes (Scriber et al., 1989).

Geographic variability in host preferences and larval performances has been identified in various local populations of swallowtail butterfly larvae during the 1980s and 1990s (Scriber, 1988; Scriber et al., 2002b) with a sharp dichotomy in survival abilities at the middle of the hybrid zone. Other variation caused by unknown local phytochemical mosaics may exist for the distinct northern and southern isolates of tulip trees from Pleistocene glaciations and recent hybrid intermediates where these plant taxa meet (Sewell et al., 1996), but we have not systematically examined this possibility. However, we have seen introgressive hybridization of the *Papilio* herbivores north of the historical center of the hybrid zone during the past few years, with global warming (Hughes, 2000; Figure 1). Apparently, less introgressive hybridization has occurred southward of the zone, perhaps due to strong selection gradients of high summer temperatures that select against the *P. canadensis* genome south of this area (Scriber et al., 2002b). Selection against increased hybridization and introgression of aspen detoxification capabilities southward of the old hybrid zone center (Figure 2) may therefore be unrelated to the low densities and availability of that plant species.

Transgenic plants and gene flow

Transgenic insecticidal cultivars have impacts analogous to classical host plant resistance terminology of 'antibiosis' (Gould, 1998). Even 'partial resistance' can slow herbivore growth, enhancing effectiveness of natural enemies. Refuges (non-toxic crops) could slow the evolution of resistance to insecticides, preserving susceptible traits as a resource.

Escape of crop transgenes is possible into wild relatives via hybridization, but at variable (low?) rates (Hails, 2000). Hybridization can be limited (using terminator technology for seeds) but not contained. Also, when closely-related viruses infect transgenic plants, they could recombine with the mRNA of the transgene, to possibly produce novel virulent (pathogenic) genotypes (Hails, 2000). Experimental studies are now possible with specific variants (single inserted novel gene) that permits determination of their affects on plant reproductive success and survival and changes in gene frequencies along environmental gradients. For example, transgenes may regulate diapause of insects, which could affect emergence and flight times and speciation (Tatar, 2000). Perhaps the only thing more difficult than predicting transgenics (GMOs) is determining the factors involved in 'risk perception' by humans (Peterson, 2000; Scriber, 2001).

Summary

Laboratory and long term field studies of 'model systems' greatly aid in deciphering some of these aesthetically-appealing but enigmatic insect-plant interactions. Several different examples have been developed and sequentially updated at the SIP conferences. While adaptive variation must ultimately be evaluated in natural environments (Mitton, 1998; Mousseau et al., 2000), we still require iterative experimental lab studies to evaluate many mechanistic aspects of insect-plant interactions. Various traits of ecological/evolutionary significance (especially those that are sex-linked; Hagen & Scriber, 1995; Prowell, 1998) and abiotic environmental dynamics shape local mosaics of host affiliations and other trait clines in a complex fashion. In fact, we have illustrated that the 'resistance' trait for detoxifying tulip tree segregates and moves into other populations independently of the butterfly species it has generally been assumed to reside within and independent of the availability of the plant. This type of geographically extensive and differential trait introgression via introgressive hybridization is uncommon, and poorly investigated (Martinsen et al., 2001).

It seems that our ability to generalize about universal patterns or fundamental underlying biotic and climatic mechanisms constraining or enhancing these processes (including feeding specialization and speciation) has been precluded, primarily by the very biological diversity and environmental variability that initially attracted most of us to these evolutionary ecology studies. A broad perspective on life history traits and their genetic linkage relationships must be considered in order to understand the various selection pressures (other than those imposed directly by the host plant phytochemistry and the associated community of natural enemies) and how they determine potential constraints and opportunities shaping the patterns of variation in the insect-plant interactions that we witness.

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