CHAPTER 6

GENETIC DIVERSITY OF *STRIGA* AND IMPLICATIONS FOR CONTROL AND MODELING FUTURE DISTRIBUTIONS

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The current knowledge of genetic diversity of *Striga asiatica*, *S. hermonthica,* and *S. gesnerioides* is reviewed. The genetic variability of these species has not been sufficiently evaluated relative to their wide distributions. Genetic diversity is a result of hybridization, clinal variation, local adaptation, and frequent colonization events. Colonization events of autogamous species formed genetically uniform populations. There is a general correlation between geographic distance and genetic distance and evidence of host specific *Striga* populations. The genetic diversity inherent in *Striga* is extremely important for modeling its future dispersal in light of global climate change. Under present day climate conditions, ecological niche models predict *Striga* species as serious agronomic threats to tropical and subtropical regions including the Western Hemisphere. Future climate change scenarios may result in an overall reduction in spread of *Striga* species in tropical and subtropical habitats with modest expansion in temperate regions.

1. Introduction

The genus *Striga* (witchweed) along with other parasitic genera once placed in the Scrophulariaceae are now considered part of the Orobanchaceae.[1,2] Crops with some measure of resistance are being integrated into *Striga* management programs. However, new *Striga* resistant crops are immediately challenged by the *Striga* seed bank. The massive seed bank precludes cropping in some areas,[3,4] is structured temporally, and represents several generations of plant parasites.[5] In addition crop breeders must cope with the diversity of species within the genus.[6,7] Although *S. hermonthica, S. asiatica,* and *S. gesnerioides* may constitute the greatest economic threat to agriculture, other species should not be ignored because they act as a reserve of genes via hybridization, as documented in fertile *S. aspera* X *S. hermonthica* crosses.[8]

The spread of witchweed throughout much of Africa as well as other parts of the world shows that rapid movement and gene flow are the norm. These dispersal events are agricultural in origin with the transport of contaminated crop seed or via livestock.[9] Economically important *Striga* species have broad distributions across Africa and Asia, setting conditions for genetically structured populations based on geographic clines. Locally adapted *Striga* races have long been observed that specialize on particular crops.[10] Thus, several factors contribute to genetic diversity in *Striga*: (1) a persistent seed bank of several generations of witchweed populations; (2) hybridization; (3) broad geographic distributions; (4) long distance dispersal; (5) and locally adapted host races. Consequently, a *Striga* resistant crop must be able to cope with the great potential genetic diversity within each *Striga* species, a condition difficult to address.

Since the advent of techniques to estimate genetic diversity, workers have focused on delineating morphotypes, hybrids, local races, and general genetic diversity within the genus. Allozyme electrophorisis was the first method of choice for investigating genetic diversity in *Striga* a few decades ago.[11] Unlike some PCR based techniques allozyme markers are co-dominant, and thus heritability can be inferred. However, allozymes generally underestimate genetic variability because less than 50% of nucleotide substitutions result in polymorphic loci.[12] Allozyme markers have largely been supplanted by polymerase chain reaction (PCR) based fingerprinting techniques. Allozyme and recent PCR based techniques are usually coherent if not directly comparable.[12,13] A variety of PCR based techniques have been applied to investigations of *Striga*, including randomly amplified fragment length polymorphism (RFLP) and amplified fragment length polymorphism (AFLP). Again issues of correlation between different PCR based fingerprinting techniques have been raised, particularly for reproducibility across time and space. Nevertheless, comparisons of RAPD, RFLP, AFLP, and other PCR based results correlate for estimates of genetic distances and variability within and among populations.[14]

The primary goal of this paper is to summarize the genetic variability of *S. asiatica*, *S. gesnerioides*, and *S. hermonthica*. Initially each species will be discussed separately, considering what is known of within and among population genetic diversity, relationships between geographic and genetic distance, methods used to measure genetic diversity, and the study areas relative to the overall distribution of the species. Then we present a synthesis of our understanding of the genetic diversity underlying the *Striga* plague in Africa in the context of predicting and modeling new *Striga* infestations in the face of global climate change. The invasive potential of *Striga* into new areas as inferred from ecological niche modeling is also presented.

2. Genetic studies

2.1. Striga asiatica

Striga asiatica is located in the African agroecosystems and natural habitats from portions of southern (including Madagascar), central, and western Africa.[7] *Striga asiatica* is also found across India and southeast Asia.[15] The taxonomic and phylogenetic relationships between plants known as *S. asiatica* in Asia and Africa need to be studied because that name has been applied to a broad geographic range and variable taxa. Populations have been found in areas outside of its typical range, for example the disjunct Mediterranean population in the Nile Delta, mediated by movement of contaminated grains. *Striga asiatica* is reported to be mainly autogamous, this is noteworthy because breeding system can strongly influence genetic structure.[16] The first study to use allozymes to investigate genetic diversity within *Striga* was for a *S. asiatica* introduction in the southeastern United States. All individuals sampled using 18 enzymes and 32 loci were monomorphic, suggesting that the entire US population was the result of a single colonization event.[11]

An AFLP study of 14 populations of *S. asiatica* in Benin, indicated genetic structure within and among populations with genetic distances of 0.028–0.038 and 0.019–0.088, respectively.[17] This is one of the most thorough studies of *Striga* genetic diversity to date. A significant regression was present (R^2=.61) between geographic and genetic distance.[17] Both findings are congruent with expected genetic structure for autogamous plants.[16] The results of Botanga *et al.*[17] support the notion of locally adapted *Striga* ecotypes based on their analyses of geographically distant populations and floral morphotypes.

AFLP was used to examine genetic diversity in 17 coastal populations of *S. asiatica* in Kenya.[18] Unlike the previous study, they found little evidence of within or among population structure, genetic distances for populations of *S. asiatica* ranged from 0.009 to 0.116 (mean of 0.032). Moreover, no relationship was observed between geographic distance and genetic distance suggesting high levels of gene flow with the more recent spread of contaminated crops.[18]

2.2. Striga gesnerioides

Striga gesnerioides has the greatest distribution of all *Striga* species across Africa with extensions to Arabia and Asia between 33°10’N and 32°15’S.[7] It is an important pest of cowpea and other dicotyledons. As an autogamous species it is no surprise that several host specific strains of *S. gesnerioides* have been recognized, but they lack morphological discontinuity.[19] Allozyme techniques were first applied to *S. gesnerioides* to investigate host specific partitioning of parasite genotypes after sowing a single Niger seed (*Guizotia abyssinica*) source on two lines that had been growing in cowpea fields.[20] Significantly different ranges of parasite genotypes were observed on each cowpea line, showing selection for virulence.[20] In the only molecular genetic study on *S. gesnerioides* AFLP markers were used to examine the genetic diversity and parasite/host interaction of four populations of introduced *S. gesnerioides* parasitic on *Indigofera hirsuta* in central Florida.[21] These were compared to *S. gesnerioides* parasitic on *I. hirsuta* and cowpea from West Africa.[21] There was a high degree of genetic uniformity for the introduced *S. gesnerioides* population of central Florida, all but one of the 71 plants sampled were identical (genetic distances 0.000–0.067), suggesting a single introduction of *S. gesnerioides* in the United States or a host driven selection. The Florida strain and the West African strain parasitic on indigo were more closely related to one another (genetic distances 0.214–0.274) relative to the Florida strain and the West African strain parasitic on cowpea (genetic distances range 0.320–0.390). Remarkably, the Florida *S. gesnerioides* was stimulated to germinate by root exudates from cowpea varieties known to be susceptible to *S. gesnerioides* in West Africa but the *Striga* failed to attach.[21,22] These results suggest that *S. gesnerioides* is presently an unlikely agronomic pest in the United States.[21] Because it is a weed of disturbed areas it is not unlikely that this strain could show a shift in host preference and spread to agroecosystems. Questions of how many genes separate strains of *S. gesnerioides* specific to agronomic versus wild hosts and how long ago strain divergence occurred remain to be answered. Currently, no studies have described the relationship between genetic distance and geographic distance in *S. gesnerioides*. However, the large number of host specific strains of *S. gesnerioides* (Chapter 9), its wide geographic range, and the findings of the studies above[20,21] indicate that genetic structure differences are quite probable across the continent.

2.3. Striga hermonthica

Striga hermonthica is mainly distributed from Senegal to Ethiopia and south to Tanzania. Collections have been made in many other areas of Africa including the Nile Delta and Namibia, and likely represent more recent introductions.[7] *Striga hermonthica* is an obligate outcrosser [23] and its hybridization events with other *Striga* species have caused some taxonomic confusion.[8] The first study of genetic diversity in *S. hermonthica* used allozyme electrophoresis (9 loci coding 8 enzymes) on samples from two populations in Burkina Faso, one adapted to pearl millet and one adapted to sorghum and one population adapted to sorghum from the Sudan.[24,25] There was a high heterozygosity within each population (H=0.261-0.365).[24,25] Within population variability was larger than the mean values for other obligately outcrossing species.[16,26] Nevertheless, Bharathalakshmi *et al.*[24,25] suggested that the extremely high fecundity/seed set in *S. hermonthica* may be a contributing factor. Their data also showed that geographic distance played a more important role in genetic differentiation of *S. hermonthica* populations than host specialization.[24,25]

Gel electrophoresis (2 DNA loci) was used to study genetic diversity and host specificity in 14 populations of *S. hermonthica* parasitizing sorghum, pearl millet, maize, and wild grasses in Burkina Faso (9 populations), Mali (4 populations), and Niger (1 population).[27,28] The results indicated low allelic divergence within populations, suggesting that the outcrossing populations were in Hardy-Weinberg equilibrium for most populations. Allelic frequencies were expected to remain constant from generation to generation in these populations. There were slight geographic distance effects and little or no host specificity effects on genetic variability, indicating low selectivity for hosts may be the trend in *S. hermonthica*.[27,28] However, the low number of loci investigated undermines any strong conclusions.

Contrasting results were presented using gel electrophoresis (14 loci in 8 enzyme systems. High levels of genetic diversity were apparent among six West African (Benin, Mali, and Burkina Faso) and nine Kenyan populations of *S. hermonthica*.[29] Again geographic distance was the primary driver of genetic differentiation with no differentiation by host.[29] RAPD markers showed higher levels of genetic diversity within *S. hermonthica* relative to *S. aspera* and their hybrids.[8] The low similarity between *S. hermonthica* and *S. aspera* (55% similarity) as measured by RAPD clearly delimits the two species.[8]

Koyama[30] conducted the first study to combine allozyme electrophoresis (47 loci in 10 enzyme systems) and RAPD markers (33 loci with five primers) to investigate genetic diversity of *S. hermonthica*. She surveyed populations from two sites in Mali and one site each from Nigeria and Kenya. Using cluster analyses with both methods showed high levels of genetic distance between geographic locations, with allozyme variance estimates of between 3.908–6.882 and RAPD variance estimates of 5.725–8.789.[30] Unfortunately, these results must be interpreted with caution. *Striga* plants were not sampled from their respective populations *in situ*, but were reared from bulked seed (from each population) sown on potted *Sorghum* in a controlled experiment.[30] Thus, the results reported do not reflect actual population genetic diversity, but genetic diversity within the individuals selected for by the strain of *Sorghum* used in the experiment and the experimental conditions applied.

This oversight is surprising because in a related study, Koyama[31] applied the same allozyme and RAPD markers to demonstrate strain specific forms of *S. hermonthica* on five *Sorghum* cultivars.[31] Finally, an AFLP analysis of genetic diversity for 24 populations of *S. hermonthica* from Kenya showed genetic distance values range from 0.007-0.025, very low genetic diversity, and no geographic distance to genetic distance relationship was detected.[18] The observed homogeneity of the Kenyan populations of *S. hermonthica* may be in part due to colonization (a founder event) from the Lake Victoria basin east into Kenya and its allogamous breeding system.[18]

2.4. Synthesis of Genetic Diversity Studies

Colonization events, linkage with agroecosystems/hosts, geographic clines, and hybridization are the central drivers of genetic diversity in *Striga*. Studies of *S. asiatica*[11] and *S. gesnerioides*[21] colonization events in the United States both showed genetic uniformity in introduced populations, suggesting single successful colonization events. This is consistent with the low genetic diversity in the relatively recently introduced Kenyan *S. asiatica* populations,[18] which is particularly remarkable for an autogamous species. Of the studies reviewed many did not demonstrate strong correlations of allozyme or PCR based markers with host-specific *Striga* strains.[24,27,29] However by combining pot studies and higher resolution of AFLP techniques, Botanga *et al.*[17] showed host specialization of *S. asiatica* in Benin. Moreover with the same combination of techniques Botanga and Timko[21] demonstrated convincingly that the introduced strain of *S. gesnerioides* in Florida (USA) is unable to effectively parasitize cowpea. Taken as a whole this suggests that allozyme markers were insufficiently variable at the scale used to identify host specific genotypes relative to AFLP.

The studies reviewed indicated a relationship between geographic distance and genetic distance.[17,21,24,30] Exceptions are attributable to either insufficient markers/loci to detect differences[27] or sampling of a relatively small geographic area, or a recent parasite introduction.[18] However with adequate markers significant correlations between geographic and genetic distances were observed in an area as small as the Republic of Benin for *S. asiatica*.[17] With a total of 30 or more species of *Striga* in Africa the storage of virulence genes in 'wild' *Striga* congeners is very real danger as evidenced by the RAPD and breeding study of the *S. aspera* and *S. hermonthica* hybrids.[8]

The genetic variability of *Striga* species has not been evaluated in depth relative to their total current distributions. Practical issues of cost and accessibility have prevented continent wide studies of genetic diversity of *Striga*. However, it should be evident that crop breeding efforts towards obtaining resistant cultivars must take the view that *Striga* species are diverse at the intraspecific level.[31] Future matching of resistant crops with resident *Striga* strains must be considered with directed quarantine efforts to prevent movement of virulent strains of *Striga*. We also consider that the genetic diversity inherent in *Striga* may be extremely important for modeling of future dispersal events in light of global climate change. Maximum and minimum germination and flowering temperatures need be recorded for *Striga* ecotypes particularly at the climatic extremes of their ranges. These basic data are clearly lacking to effectively predict the worst case yet unlikely scenarios of dispersal events.

3. Ecological Niche Modeling and Invasive Potential of *Striga*:

We used ecological niche modeling to predict the invasive potential of three *Striga* species which constitute the major agronomic threats.[32] The software used to generate the models was the Genetic Algorithm for Rule-Set Prediction (GARP).[33,34] Under current climate conditions, the ecological niche models predicted great invasive potential of *Striga* species that extends to tropical and subtropical regions worldwide including the Western Hemisphere (Fig. 1). The rainforest climatic conditions fall within the range favorable to *Striga* germination and development. However, the deep Amazon Basin rainforest (and other similar communities) is excluded because climatic conditions are not favorable for germination, as witchweeds are shade intolerant and

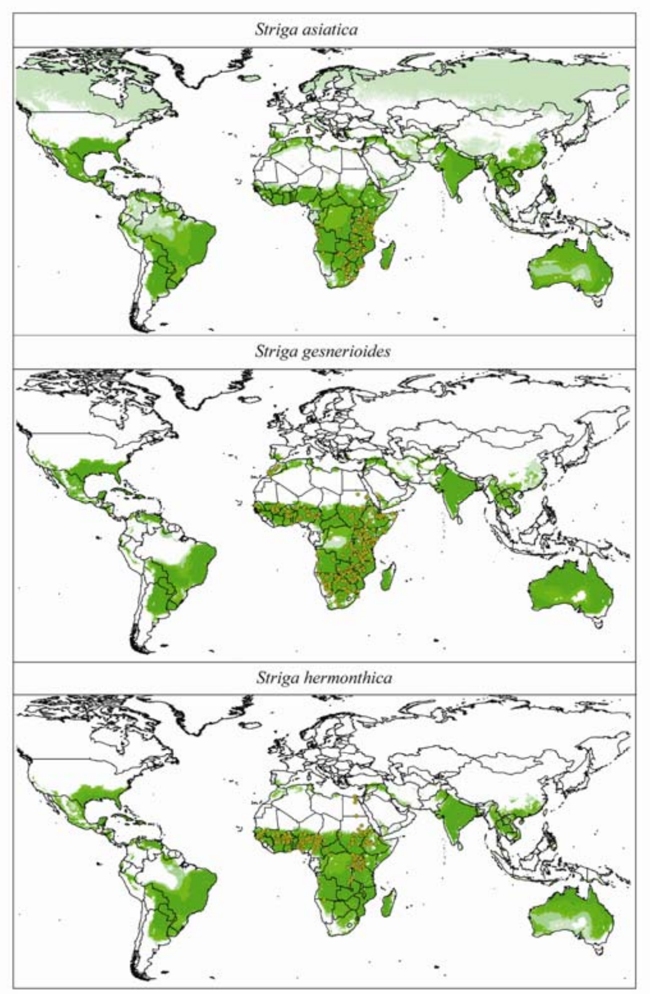

Figure 1. Output of ecological niche models for *Striga asiatica*, *S. gesnerioides*, and *S. hermonthica* under current climatic conditions. Darker shading indicates higher likelihood of current and future distributions. Present African distribution indicated with dots.

germination is retarded in wet and poorly aerated soils (wet dormancy). The invasive potential of *Striga* will likely increase in tropical Western Hemisphere with increasing disturbance, logging activity, and expansion of soybean farms and other potential hosts in this region. Recently, Brazil witnessed a huge expansion in farming at the expense of natural habitats increasing the risk of *Striga* infestation.

Our models showed that *Striga* should exhibit a worldwide expansion in savannas dominated by typical *Striga* hosts such as grasses and herbaceous plants (Fig. 1).[32] Movement of goods, people, other weed species, farmers' saved seeds in addition to the "informal" crop seed market could facilitate *Striga* spread. The southeastern United States is predicted as a suitable region for all *Striga* species consistent with the accidental introduction of *S. asiatica* in the Carolinas and more recently of *S. gesnerioides* in Florida.

Striga hermonthica, *S. gesnerioides*, and *S. asiatica* are well known for their impressive abilities to adapt to different habitats and agroecosystem by developing host-specific strains and ecotypes across their ranges.[15] *Striga hermonthica* and *S. gesnerioides* have evolved host-specific strains that tolerate extreme conditions in the semi-arid regions. Under these conditions, *S. gesnerioides* has evolved specificity to *Euphorbia* species.[35] *Striga hermonthica* has evolved and attacked pearl millet. Because of their adaptation to drought, these two species range the farthest north among *Striga* in Africa and can cause severe damage as their hosts are already stressed. *Striga hermonthica* can attain 50% germination and was successfully conditioned and germinated under conditions described as permanent wilting points for most other plants.[36] In addition, it tolerates wide ranges of day/night temperatures between 40/30º and 25/15ºC. These broad climatic tolerances render *S. hermonthica* a dangerous parasite throughout its range. Aigbokhan *et al.*[8] suggested that *S. hermonthica*, an aggressive agroecosystem pest, is a species recently derived from *S. aspera* which is most commonly restricted to grassland savanna. Moreover *S. aspera* itself has been reported to attack rice and maize in Ivory Coast.[37] *Striga asiatica* is the most widespread of all witchweeds.[15] Based on herbarium studies, it has a wider geographical range with more diversified habitats and a greater host range than previously thought. Unfortunately, the taxonomy of the

S. asatica complex has been confused for some time.[7] It is essential that workers always deposit voucher specimens in accessible herbaria so that the plant identity can be verified. More basic taxonomic work remains to be done in the *S. asiatica* complex because of its widespread transcontinental distribution.

The potential presence of witchweeds in temperate regions is greatly reduced by the inability of their seeds to germinate, successfully attach, or reach maturity and set seeds under the climatic conditions in these ecosystems. Optimum temperatures for seed germination of most *Striga* spp. are 30-35ºC.[38] In most studied species, germination percentages were very low at or below 20ºC, even when the conditioning period was prolonged.[39] For example, under lab conditions, the germination percentage in the American *S. asiatica* was only 0.5% in seeds conditioned for 15 days at day/night temperatures of 20/14ºC, compared to 37% germination after 2 days of conditioning at a day/night temperature of 32/26ºC.[39] The minimum day/night temperature under which the American *S. asiatica* infecting maize can successfully flower is 29/23ºC. The climatic conditions in the midwestern USA Corn Belt fall within the range tolerable to witchweeds. However, the day/night temperatures in the northern USA Corn Belt States are below that required for germination/flowering of witchweed.[39] These findings were consistent with the predictions of the ecological niche models (Fig. 1).

Future climate change may have a profound effect on geographic distribution and invasive potential of many plant species including root parasites. Early projections suggested many plants may have broader geographic potential for invasion.[40] This idea has not been quantitatively tested. One study however indicated broader invasive potential in changing climates[41] but another model[42] predicted overall reduction in potential distributional area of invasive species with the potential for some regional expansions. Our preliminary predictions for *Striga* invasive potential under future climate change scenarios support the notion of Roura-Pascual *et al.*[42] for possible overall reduction in potential distribution and spread of *Striga* species (Mohamed and Peterson, unpublished). Ecological niche models indicate a loss in potential distributional areas for *Striga* in tropical and subtropical habitats with modest expansion in temperate regions, especially in North America.

These are welcoming results for badly impacted regions in Africa though it could be too late then.

In conclusion, our genetic algorithm based models suggest that changing climate will play major roles in determining geographic distributions of *Striga* directly by affecting germination, growth, and development, or indirectly through its hosts. The problems of *Striga* mostly affect small hold farmers in the developing world as they are unable to adopt expensive chemical control or use modern agricultural practices and because they depend on precisely those crops hardest hit by these parasites. In dry regions of the developing world, parasitic weeds take a large toll because of the limited number of crops that can be cultivated. Eradication programs require significant commitments of labor and financial resources over a long period of time and work only with limited infestations. For example, the United States took over 50 years and >$250 million to contain/eradicate *S. asiatica*.[43] This was a small investment compared to potential losses in corn production if *Striga* were to spread to the Corn Belt. In the United States, crops threatened by witchweeds are valued at $20 billion annually. The American experience is indeed a model for containment/eradication of parasitic weeds. It involved many logical steps that culminated in containment and eventually eradication. For an excellent review of the problems of invasives and containment see references 32, 44, and 45. Again, problems with witchweeds could be compounded by climate change, which may result in new invasions in regions anticipated to have temperatures and moisture within the ranges tolerated by witchweeds. Genetic diversity studies of *Striga* species while still not comprehensive or continent wide in scope still suggest locally adapted and host specific genotypes in some African agroecosystems. In light of changing global climate these data should be warning enough to underscore the differential invasive potential of certain genotypes within a *Striga* species. We suggest that the genotypes with the greatest potential for invasion into new systems need to be identified and tested empirically under simulated current and projected climatic conditions. We hope that this may allow us to more finely predict and marshal energy against future invasions.

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