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Global Invasive Potential of 10 Parasitic Witchweeds and Related Orobanchaceae

The plant family Orobanchaceae includes many parasitic weeds that are also impressive invaders and aggressive crop pests with several specialized features (e.g. microscopic seeds, parasitic habits). Although they have provoked several large-scale eradication and control efforts, no global evaluation of their invasive potential is as yet available. We use tools from ecological niche modeling in combination with occurrence records from herbarium specimens to evaluate the global invasive potential of each of 10 species in this assemblage, representing several of the worst global invaders. The invasive potential of these species is considerable, with all tropical and subtropical countries, and most temperate countries, vulnerable to invasions by one or more of them.

INTRODUCTION

The parasitic angiosperm genera *Aeginetia*, *Alectra*, *Orobanche*, and *Striga* are the most serious parasitic weeds in the world today. Along with *Cuscuta* (Cuscutaceae), they represent the five parasitic plant genera on the list of noxious weeds maintained by the United States. These genera are classified in the family Orobanchaceae (1), which are obligate root parasites, in that they require host plants to complete their life cycles. Broomrapes (*Orobanche* spp.) and *Aeginetia* are holoparasites, which entirely lack chlorophyll and depend on hosts for nutrition. The other genera, considered hemiparasites, have some chlorophyll and are capable of photosynthesis, but they still rely on hosts for water and minerals.

Worldwide, more than 30 species of witchweeds (*Striga* spp.) are recognized, 22 of which are endemic to Africa (2), the center of distribution and diversity of witchweeds. All known *Striga* species are African except *S. curviflora* Benth. (Australia, New Guinea), *S. densiflora* (Benth.) Benth., *S. sulphurea* Dalz. ex Dalz. & Gibbs (India), *S. multiflora* Benth. and *S. parviflora* Benth. (Australia), and *S. masuria* (Buch.-Ham. ex Benth.) Benth. (= *S. flava* Miq.?, *S. esquirolia* Lév?) (China, India, Indonesia). The most economically important *Striga* species are also native to Africa, where *Striga* species occur throughout the continent, with greater diversity in the grassland savannas north of the equator. Invasive *Striga* populations are found in the Arabian Peninsula, South Asia, Australia, and the United States (2).

Orobanche includes more than 100 species in both the eastern and western hemispheres, and reaches its greatest diversity in the Mediterranean region and western Asia. Most economically important *Orobanche* species are native to the eastern hemisphere (3). Invasive *Orobanche* populations extend to North America, South Asia, Southeast Asia, Southern Africa, and Australia. *Alectra vogelii* Benth. and *Aeginetia indica* L. represent the two other genera in this study, and are restricted to Africa and Asia, respectively.

Striga and Orobanche impose severe constraints on cereal and legume production worldwide. *Striga* are pernicious weeds that attack cereals and legumes, causing great yield losses, especially in sub-Saharan Africa and arid areas of South Asia.

S. gesnerioides (Willd.) Vatke occurs throughout Africa, perhaps thanks to its ability to develop host-specific strains, each with a narrow host range. Indeed, Mohamed et al. (2) described eight host-specific strains, the most economically important being those attacking cowpea (*Vigna unguiculata* (L.) Walp.) and tobacco (*Nicotiana tabacum* L.). Other strains are reported on diverse wild dicot plants of no commercial value, including a strain found in the southeastern United States. *S. gesnerioides* causes severe damage to cowpea in West Africa, has caused problems on tobacco in localized areas in southern Africa, and was recently reported on sweet potato (*Ipomoea batatas* (L.) Lam.) in East Africa (4).

All other witchweeds considered in this study are capable of parasitizing sorghum (*Sorghum bicolor* (L.) Moench), maize (*Zea mays* L.), pearl millet (*Pennisetum glaucum* (L.) R. Br.), rice (*Oryza sativa* L.), and sugar cane (*Saccharum officinarum* L.). The most destructive witchweeds are native to Africa, including *Striga hermonthica* (Del.) Benth., *S. asiatica* (L) Kuntze (*sensu stricto*), and *S. gesnerioides*. *S. hermonthica* is a serious pest to cereal production (sorghum, maize, millet, rice), especially in the Sahel region (Senegal to Ethiopia), where it has developed two host-specific strains: one specific to millet, occurring in the drier and more northerly region of the Sahel; and another that attacks sorghum and is found farther south, in wetter regions. *S. hermonthica* has been reported to cause 70 to 100 percent crop loss in maize, sorghum, and pearl millet in Nigeria (5). *S. asiatica* is common in southern and central Africa, and in localized areas in West Africa, causing severe damage to sorghum, maize, and millet. *S. hirsuta* Benth. and *S. lutea* Lour., closely related to *S. asiatica*, are primarily confined to natural grasslands, but they have the ability to attack crops (see [2] for information on this species complex).

Broomrapes (*Orobanche* spp.) are native primarily to the Mediterranean region (i.e. North Africa, the Middle East, and southern Europe), and western Asia, where they cause significant crop damage. Important hosts of broomrapes are as follows: *O. crenata* Forskal is common on garden pea (*Pisum sativum* L.), lentil (*Lens culinaris* Medik), faba bean (*Vicia faba* L.), and garden vetch (*V. sativa* L.) around the Mediterranean basin; *O. cernua* Loeft. is common on carrot (*Daucus carota* L.), tomato (*Lycopersicum esculentum* Mill.)**,** and tobacco (*Nicotiana tabacum* L.) in the Mediterranean basin extending eastward into Europe and Asia; *O. cumana* Wallr. is common primarily on sunflower (*Helianthus annuus* L.) in sunflower-growing countries in the Mediterranean basin, Eastern Europe, and countries of the former Soviet Union; *O. ramosa* L. is common on rape (*Brassica napus* L.) and many hosts in the Solanaceae family including eggplant (*Solanum melongena* L.), tomato, tobacco, and potato in the Mediterranean region, Europe, Asia, Africa, and the United States (a review of parasitic weed problem and control can found in [4]).

Broomrapes are as destructive as witchweeds. For example, Bernhard et al. (6) studied the relationship between *Orobanche* seed numbers and crop losses in Israel. They found that yield losses due to *O. crenata* in peas were 100 percent at high infestations, and approximately 50 percent in carrots when *O. crenata* and *O. aegyptiaca* Pers. were present in moderate infestations (~200 seeds/kg of soil).

The other two genera treated herein, *Aeginetia* and *Alectra*, are comparatively less common: *Alectra* includes about 30 species occurring primarily in tropical and subtropical Africa. The most economically important species is *A. vogelii*, which attacks cowpea and peanut (*Arachis hypogaea* L.) in Africa, with high crop losses reported for Botswana, Ethiopia, and Mali (4). Bambara (*Vigna subterranea* [L.] Verdc.) and mung bean (*V. radiata* [L.] R. [Wilezek]) are also damaged in parts of eastern and southern Africa. Other important species include *A. fluminensis* (Vell.) Stearn, found in tropical and subtropical South America on sugar cane, and *A. pica* (Hiern) Hemsl., reported to attack cowpea and peanut in Ethiopia and cowpea in Cameroon (7). *Aeginetia indica*, one of about four species of *Aeginetia*, is native to India, Indonesia, and the Philippines, and is known to attack sugar cane and cereals in South Asia. Other species of *Aeginetia* are not reported to attack cultivated crops.

More generally, the ability of these parasitic Orobanchaceae to produce high numbers of seeds (up to 500 000 seeds per plant per year in *Striga*) results in enormous seed reserves in soils that can be triggered to germinate and damage crops even before host plants emerge above ground. Also, Orobanchaceae weeds are host-specific, and seeds may remain in the soil for decades awaiting the correct host. *Orobanche* and *Striga* are widespread in the eastern hemisphere, affecting productivity of many crops—indeed, the area infested by *Striga* is increasing: Berner et al. (8) estimated that in West Africa alone 20×10^6 ha in cereal production are severely infested, and 70×10^6 ha are moderately infested by *Striga* at a cost of $7 thousand million yearly, affecting more than 100 million people. *Orobanche* threatens 16×10^6 ha in the Mediterranean region and western Asia; together with *Striga*, they infest 4.5 percent of land available globally (9). In Africa and South Asia, crop seeds become contaminated, for example, when maize is extended on the ground to dry, constituting a major form of *Striga* dispersal. Other means of dispersal include contaminated soil, wind, cattle, and human movements, all of which facilitate the spread of these weeds within and between countries (10). Control measures involve rotation with trap crops, intercropping with legumes, use of *Striga*-tolerant varieties, early planting, application of heavy dosages of fertilizations and green manure, use of herbicides, development of resistant varieties, solarization, and even hand weeding (4). In many infested areas, integrated control is practiced and has been effective (11, 12). The least expensive control measures are those devised on the basis of prediction, prevention of invasion, early detection, and containment.

Ecological niche modeling (13) offers a fascinating view into potential geographic distributions of species (14, 15). Briefly, ecological requirements of species are estimated on the basis of patterns of presences and absences across native distributional areas, and once they have been validated these requirements can be used to examine other landscapes (e.g. other continents) for regions meeting the species' ecological profile, and thus fitting its potential distribution. The method has seen extensive exploration and testing using a variety of analytical techniques, and application to diverse questions and biological systems (16–18). Native-range ecological characteristics provide excellent predictability regarding the geographic potential of species as invasives—in short, species generally obey the same ecological rules on their invaded geographic ranges as on their native geographic ranges (15).

Curiously, no global evaluation of invasive potential has been developed for any of the parasitic weed species. Considering the economic impact of these species, this exercise could be invaluable in their management. In this paper, we develop ecological niche models for 10 species of plants in the Orobanchaceae (1 *Alectra*, 1 *Aeginetia*, 3 *Orobanche*, and 5

Striga) known to be aggressive weeds, and project the models worldwide to evaluate their invasive potential. The result of these analyses is an indication of broad invasive potential into essentially all tropical and subtropical countries, and many temperate countries as well. We discuss our results in terms of risks of introduction, potential for spread, and possibility of avoidance of introductions.

METHODS

Input Data

Herbarium collections with specimens of species of interest were studied to obtain range occurrence data suitable for retrospective georeferencing. Specimen data were drawn from the Missouri Botanical Garden, Harvard University Gray Herbarium, New York Botanical Garden, Royal Botanical Gardens (Kew, UK), National Botanic Garden (Brussels, Belgium), Natural History Museum (London), and Muséum National d'Histoire Naturelle (Paris). Altogether, we obtained 19–272 points for each species that could be georeferenced, and that were spatially unique (i.e. not coincident with other points): 93 for *Aeginetia indica*, 50 for *Alectra vogelii*, 100 for *Orobanche cernua* Loefl. (= *O. cumana*), 91 for *O. crenata*, 136 for *O. ramosa* L., 105 for *Striga asiatica* (*sensu stricto*), 272 for *S. gesnerioides*, 190 for *S. hermonthica*, 132 for *S. hirsuta*, and 19 for *S. lutea*. Throughout this study, for *Striga* spp., we followed taxonomic arrangements proposed by Mohamed et al. (2). We realize that *O. cernua* and *O. cumana* are separate species (19) with many taxonomic complexities. We included *O. cumana* in *O. crenua* because some of our specimens may in fact be misidentified as *O. cumana*, but we discuss them separately in terms of their hosts, climatic requirements, and geographical distributions.

To summarize ecological variation across native and introduced geographic distributions of species, we used eight raster grid data sets (coverages) to summarize aspects of topography and climate. Among topographic parameters were elevation, slope, and aspect (from the US Geological Survey's Hydro-1K data set [20], native resolution 1×1 km); climate parameters included annual mean precipitation, solar radiation, annual mean temperature, annual mean minimum monthly temperature, and annual mean maximum monthly temperature (for 1960–1990 from the Intergovernmental Panel on Climate Change [21], native resolution 50×50 km). To minimize conflicts in scale between topographic and climatic data, we conducted all analyses at an intermediate resolution (10×10 km). Models were developed within rectangular areas close to species' distributional areas (central and southern Africa for *Striga* and *Alectra*, southern Asia for *Aeginetia*, and southern Europe and northern Africa for *Orobanche*), and projected to the whole world to visualize potential geographic distributions of species.

Ecological Niche Modeling

Ecological niches are herein defined as the set of conditions under which a species is able to maintain populations without immigration (22). Our approach consisted of three steps: *i)* modeling ecological niche requirements on the basis of known occurrences of native distributional areas of species; *ii)* testing the accuracy of native-range predictions using subsets of available occurrence information; and *iii)* pooling all available occurrence data to model and project worldwide to identify areas predicted to be susceptible to invasion.

The software tool used for niche modeling was the Genetic Algorithm for Rule-set Prediction (GARP) (23). GARP uses an evolutionary-computing approach to carry out flexible and

powerful searches for nonrandom associations between environmental variables and known occurrences of species, as contrasted with the environmental characteristics of the overall study area.

Specifically, within the GARP program, available occurrence points are resampled with replacement to create a population of 1250 presence points; an equivalent number of points is resampled from the population of grid squares (i.e. pixels) from which the species has not been recorded. These 2500 points are divided equally into a training data set (for creating models) and a testing data set (for evaluating model quality). Models are composed of a set of conditional rules developed through an iterative process of rule selection, evaluation, testing, and incorporation or rejection. First, a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules, etc.) and applied to the training data set. Then a rule is developed by a number of means (mimicking DNA evolution: point mutations, deletions, crossing over, etc.) to maximize predictive accuracy. Rule accuracy is evaluated via the testing data, as a significance parameter on the basis of the percentage of points correctly predicted as present or absent by the rule. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the final rule set. The algorithm runs either 1000 iterations or until the addition of new rules has no effect on predictive accuracy. The final rule set (the ecological niche model) is then projected onto a digital map of native or potentially invaded areas to identify a potential geographic distribution. Although these environmental variables cannot represent all possible ecological niche dimensions, they likely represent or are correlated with many influential ones in delineating species' potential distributions.

Spatial predictions of presence and absence can hold two types of error: omission (areas of known presence predicted absent) and commission (areas of known absence predicted present) (24). Because GARP does not produce unique solutions, we followed recently published best practices approaches to identifying an optimal subset of resulting replicate models (25). For each analysis, we developed 100 to 1000 replicate models; of these models, we retained the 20 with lowest omission error. Finally, from these 20, we retained the 10 with moderate commission error (i.e. we discarded the 10 models with area predicted present showing greatest deviations from the overall median area predicted present across all models). This best subset of models was summed to produce final predictions of potential distributions.

To validate our model predictions, we evaluated their ability to predict independent sets of test points compared with that expected under random models (24). We used a simple random assortment of data into training and testing data sets (see above). Because our final models consist of composites (sum) of 10 best subsets models (25), they have 10 levels of prediction (1–10), with 10 representing complete model agreement in prediction of presence and 0 representing complete model agreement in prediction of absence. Probabilities of observed coincidence between test points and model predictions were evaluated as the binomial probability of the observed number of successes given the proportional area predicted present at each level of prediction (26).

RESULTS AND DISCUSSION

Geographic distributions predicted for each species from the ecological niche models (Figs. 1–4) were highly coincident with known native distributions for each of the 10 species. In each case, coincidence of independent subsets of points (testing points) with predicted distributions was considerably better than the random null model (binomial tests, all $P \ll 0.05$). This result indicates that the ecological niche models hold significant predictive power for distributional phenomena related to each species at least across native ranges; as a consequence, we explored their implications for the global invasive potential of each species. For all species studied, we based our estimate of present-day established range and native geographic range on herbarium records. Although we conducted an extensive survey of most large international herbaria, this approach could nonetheless have underestimated geographic ranges of species with poor records in these herbaria.

Orobanche species are native to the Mediterranean region (3), which has a mild and wet winter, and a hot and dry summer. Temperatures are usually mild, but summer conditions can get very hot and winter conditions can approach freezing—the overall range is 0–40°C. Rainfall in this region is about 25–45 cm, most occurring in winter. The geographic range of *Orobanche* also extends into the deciduous forests of Eurasia (temperature range −30 to +30°C, annual rainfall 76–150 cm) and temperate grasslands (temperature range −40 to +38°C and rainfall 50–90 cm).

All *Orobanche* species in this study showed overall similarities in their native ranges (Fig. 1). However, *O. cernua* (= *O. cumana*) and *O. ramosa* have broader native ranges, including northern and eastern Africa, most of southern and central Europe, and western Asia, where they cause great damage to crops such as sunflower (*O. cumana*), tomato, and other Solanaceae (*O. cernua*, *O. ramosa*), among others. *O. crenata*, on the other hand, has a limited range and has been collected primarily from southern Europe and countries around the Mediterranean basin in North Africa and the Middle East where it is a threat to faba bean and other leguminous crops (Fig. 1). Projecting native-range models of *Orobanche* species to the rest of the world showed that they have great invasive potential. All analyzed species pose potential invasive threats to much of the United States, southern and eastern South America, eastern Asia, southern Africa, and southern Australia, with *O. crenata* showing a more restricted invasive potential compared with other species (Fig. 1). No doubt temperature and other physical factors influence—and in part explain—*Orobanche* distributions, either directly or indirectly through hosts. Optimum temperature for germination of *Orobanche* is affected by many other factors, including seasonal temperature, length and temperature of the conditioning period (warm period before germination), hosts, and agricultural practices. For example, the limits of the distribution of *O. crenata* could be attributed to its low and narrow range of optimum temperatures requirement for conditioning and germination, which was found to be around 18°C (27): both lower and higher temperatures resulted in poor germination. As a result, for example, in Israel, *O. crenata* (carrot and Fabaceae) was found only in winter, whereas *O. cernua* (Solanaceae) and *O. cumana* (sunflower) were found to infect their respective hosts only in summer, and *O. ramosa* affected both winter and summer crops, suggesting a temperature or host effect (28). Higher optimum temperatures for conditioning and germination (23–26°C) were reported for *O. cumana* and *O. cernua* (29, 30) and up to 28°C for *O. ramosa* (29). Eizenberg et al. (30) studied effects of temperature on resistance, and suggested that effects of temperature on *O. cumana* are complex. At higher temperatures (>27°C), they found that resistant varieties were more resistant to broomrape attack than at lower temperatures. Lower temperatures (<15°C) slowed parasite development in both resistant and susceptible varieties, but resistant varieties were only resistant at lower temperatures. Moisture could also be a factor, because *O. cernua* was found to be more restricted to arid areas in the Mediterranean basin than *O. cumana* (19). In
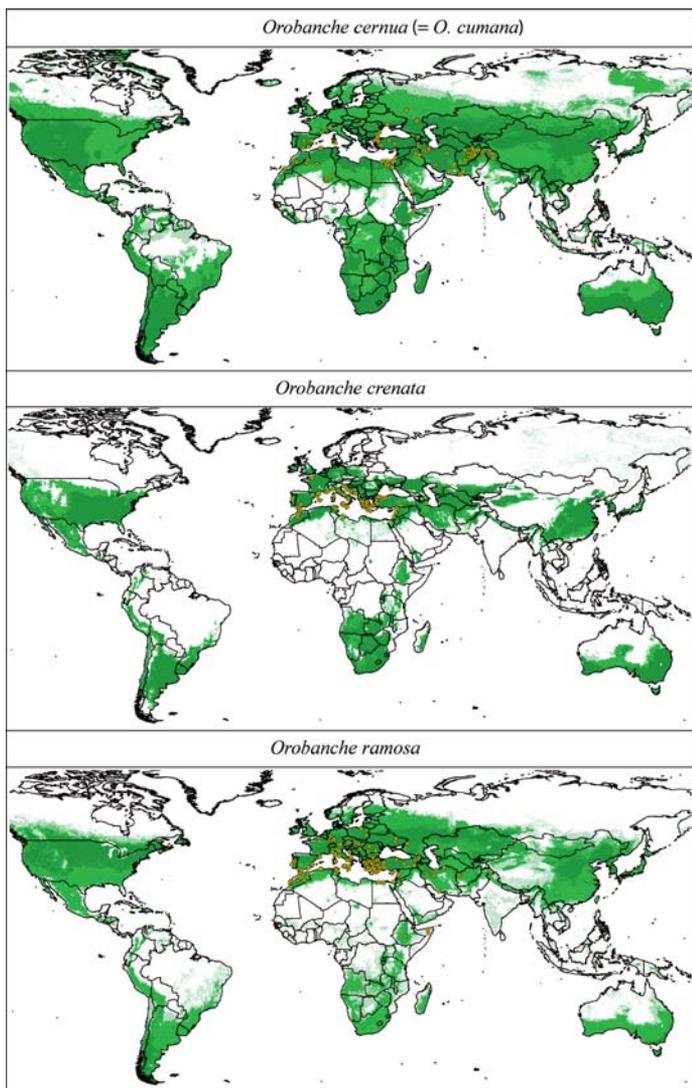
Figure 1. Summary of native-range occurrence points (dotted circles), and inferred native and global potential distributional areas of *Orobanche cernua* (= *O. cumana*), *O. crenata*, and *O. ramosa*. Color ramp for predictions from white (no model predicts potential presence) to green (all models agree in predicting presence).

all Orobanchaceae, prolonged seed conditioning leads to wet dormancy, which is more pronounced at lower than at high temperatures.

Models of predicted ranges of *Orobanche* species were highly consistent with known incidences of *Orobanche* invasions. *O. ramosa* is known to be established as invasive in, for example, California and Texas, Central America, Argentina, Nepal, southern Australia, and Southern Africa. Whereas *Orobanche* species may have been native in southern Europe along the Mediterranean coast (3), more likely they were introduced elsewhere in Europe; for example, *O. ramosa* was listed as an invasive plant in the Czech Republic (31) and very common in Bulgaria, Germany, Poland, Slovakia, and Ukraine. *O. ramosa* and *O. cernua* were known as serious pests of tomato in Ethiopia, and *O. ramosa* is damaging to oil seed rape in Morocco and southwestern France, expanding into Western Europe (4). *O. cumana* is reported primarily on sunflower in the Mediterranean basin, Eastern Europe, and the former Soviet Union. *O. cernua* is a serious pest on carrot, tomato, and tobacco in the Mediterranean basin, extending eastward into Europe and Asia. *O. crenata* is common on faba bean and other Fabaceae in the Mediterranean basin. Of all *Orobanche* species, *O. cernata* is the least expected in the United States because its hosts are not commonly grown in that country. Model

predictions omit part of the known range of *O. ramosa* in Sudan, because it is known to occur as an invasive in limited areas along the Nile River in Khartoum Province (Mohamed, unpubl. data).

With anticipated climatic changes taking the form of higher temperatures and drought in many areas of the world, *Orobanche* species could pose greater threats to agriculture by expanding their ranges farther north in Europe and elsewhere. Our models did not take into consideration these anticipated climatic changes and consequent host distributional shifts as factors affecting the distributions of parasitic weeds, but future work will incorporate them (32).

In general, *Striga* species have similar native and potential geographic ranges (Figs. 2 and 3). All five species examined are native to tropical and subtropical Africa, and have spread elsewhere (along with cultivation of their hosts) through contaminated seed stocks (2). *Striga* are known to occur in tropical, subtropical, and semiarid regions, including Africa, Arabian Peninsula, South Asia, Southeast Asia, and Australia. Wet areas within this region—rainforest—may receive high annual rainfall averaging 125–660 cm. This region is warm year-round, with average annual temperatures of 25°C, and temperatures rarely exceeding 34°C or falling below 20°C, which provides favorable temperatures for conditioning, germination, and development of all witchweeds studied (e.g., 33). In rainforest, *Striga* may occur only in open areas, because they are shade intolerant (Figs. 2 and 3), and because germination is retarded in wet and poorly aerated soils (wet dormancy). *Striga* species show greatest diversity in subtropical and tropical grassland savannas, where their typical hosts—grasses and other herbaceous plants—dominate. Annual rainfall in grasslands is 50–150 cm, and can be highly seasonal, and annual mean temperatures range from 20 to 30°C, which is within tolerable ranges for most witchweeds. Some *Striga* species have developed host-specific strains that tolerate conditions in the driest parts of this region. Under these conditions, strains of *S. hermonthica* have adapted to millet, and *S. gesnerioides* have evolved specificity to *Euphorbia* species, and can cause severe damage because their hosts are already stressed. Because of their adaptation to drought, these two species range the farthest north among *Striga* in Africa (Figs. 2 and 3).

Potential distributions of *Striga* species extend to tropical and subtropical regions worldwide, except for deep rainforest, such as the Amazon basin (Figs. 2 and 3). The model consistently predicted the southeastern United States as suitable for all *Striga* species studied. This prediction is consistent with the accidental introduction and establishment of *S. asiatica* in North Carolina and South Carolina, and of *S. gesnerioides* (Willd.) Vatke in Polk County, Florida. *S. asiatica* is reported as invasive in the tropical savannas of northern Australia (34). The species known as "*S. asiatica*" in India is widespread in South Asia, causing serious damage to cereals, but its relationship to African *S. asiatica* has not yet been studied. This species, like African *S. asiatica*, may have yellow, red, or white flowers. In addition, *S. angustifolia* Saldanha and *S. densiflora* are also damaging and widespread witchweeds in South Asia. All three have been reported to attack sorghum, maize, millet, and sugar cane in the region. *S. asiatica*, *S. gesnerioides*, and *S. hermonthica* have been reported from Yemen and Saudi Arabia (2). The other two witchweeds in this study, *S. hirsuta* and *S. lutea*, are closely related to *S. asiatica*, and showed similar distributional patterns with each other and with *S. asiatica*. Although they have the potential to attack crops, they are primarily restricted to native grasslands (2).

Three witchweeds showed great invasive potential: *S. asiatica*, *S. hermonthica*, and *S. gesnerioides* (Figs. 2 and 3). This result is not surprising because they were known to have greater ability to adapt to different habitats and agroecosystems
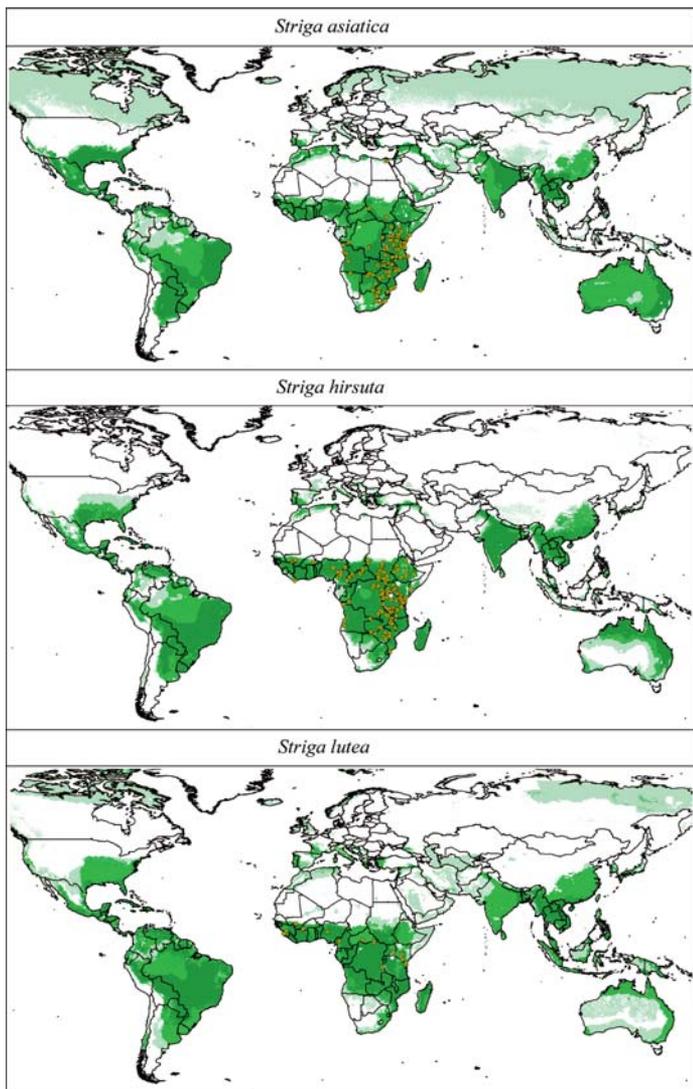
Figure 2. Summary of native-range occurrence points (dotted circles), and inferred native and global potential distributional areas of the *Striga asiatica* group, including *S. asiatica (sensu stricto)*, *S. hirsuta,* and *S. lutea*. Color ramp for predictions from white (no model predicts potential presence) to green (all models agree in predicting presence).

S. hermonthica can attain 50 percent germination in 3 d at −1.2 MPa and 30°C, and was successfully conditioned and germinated at −1.5 MPa, which is described as the permanent wilting point for most plants, and that it tolerates wide ranges of day/night temperatures between 40/30° and 25/15°C. These broad climatic tolerances make *S. hermonthica* a dangerous parasite throughout its range. *S. asiatica,* on the other hand, is common in southern and central Africa, and in localized areas in West Africa. Problems with witchweeds could be compounded by climate change, which may result in new invasions in areas anticipated to have higher temperatures and moisture within the ranges tolerated by witchweeds. Other witchweed species that may be of concern include *S. aspera* (for sorghum in West Africa), *S. forbesii* Benth. (primarily for sorghum and corn in southern Africa and sugar cane in East Africa), and *S. latericea* Vatke (for sugar cane in East Africa).

A few model results (Figs 2 and 3) suggested a broad potential geographic range of witchweeds in the southeastern United States. The potential presence of witchweeds in these areas and in temperate regions globally is greatly reduced by the inability of their seeds to germinate under prevailing climatic conditions in these ecosystems. Mature seeds of witchweeds require a period of "after ripening" in dry and warm conditions, followed by a period of conditioning in a warm and moist environment, and finally must be stimulated to germinate by their host root exudates. Optimum temperatures for germination of *Striga* seed are 30–35°C (33). In most species studied, germination percentages were very low (≤20°C), even when the conditioning period was prolonged (37). For example, under laboratory conditions, the germination percentage in *S. asiatica* (American witchweed) was only 0.5 percent in seeds conditioned for 15 d at day/night temperatures of 20/14°C, compared with 37 percent germination after 2 d of conditioning at a day/night temperature of 32/26°C (37). The same authors (37) reported that the minimum day/night temperature under which the American witchweed infecting corn can successfully flower is

by developing host-specific strains, each capable of attacking a narrow host range. Aigbokhan et al. (35) suggested that *S. hermonthica*, an aggressive agroecosystem pest, is a species recently derived from *S. aspera*, which is most commonly restricted to grassland savanna (*S. aspera* itself was recently reported to attack rice and maize in Côte d'Ivoire). These three species are also serious root parasites, capable of causing enormous damage to their hosts. Globally, the cereal grains corn, sorghum, and millet; and dicot food crops in the Fabaceae, Convolvulaceae, and Solanaceae families are all threatened by witchweeds if they were to spread to the new areas predicted by the models. Host-specific strains of *S. gesnerioides* cause severe damage to cowpea, especially in West Africa, to tobacco in localized areas in southern Africa, and (recently reported) to sweet potato in East Africa (4), even though these strains were rarely known as problems outside their regions, and the American strain of *S. gesnerioides* has not been reported to attack cultivated crops. *S. hermonthica* and *S. asiatica* are known to be serious pests to cereal production (sorghum, maize, millet, and rice) in Africa and South Asia. *S. hermonthica* is especially bothersome in the Sahel, and problems associated with it are increasing, especially in arid areas and those with poor soils. Dawoud and Sauerborn (36) showed that
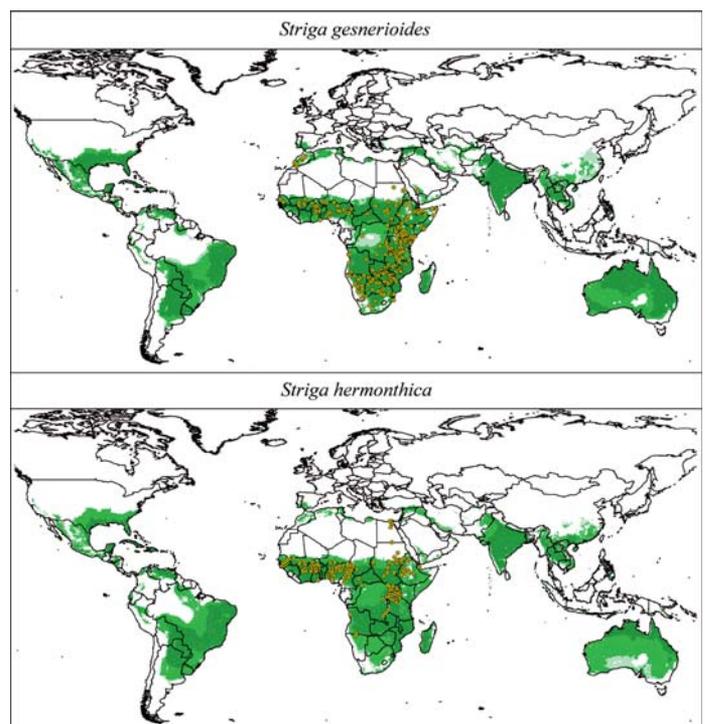

Figure 3. Summary of native-range occurrence points (dotted circles), and inferred native and global potential distributional areas of *Striga gesnerioides* and *S. hermonthica*. Color ramp for predictions from white (no model predicts potential presence) to green (all models agree in predicting presence).
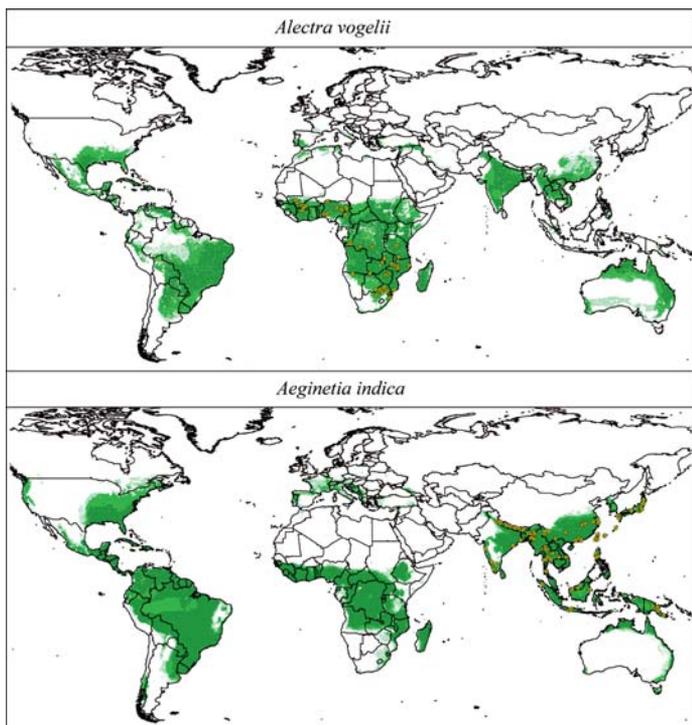
Figure 4. Summary of native-range occurrence points (dotted circles), and inferred native and global potential distributional areas of *Alectra vogelii* and *Aeginetia indica*. Color ramp for predictions from white (no model predicts potential presence) to green (all models agree in predicting presence).

29/23°C. They concluded that the growing conditions in some of the US states known as the Corn Belt (i.e. midwestern United States) are within the range in which witchweeds can grow. This suggestion is highly consistent with our model predictions, in which only the northern Midwest states, where day/night temperatures are below those required for germination/flowering of witchweed, were left out of model predictions (Figs. 2 and 3). Reid and Parker (33) reported that 23°C was a more satisfactory conditioning temperature for *S. hermonthica* than 29°C, whereas *S. gesnerioides* and *S. asiatica* showed better germination when conditioned at 33°C. The lower temperature requirements for conditioning of *S. hermonthica* seeds may suggest a greater invasive potential in temperate regions (Figs. 2 and 3).

Alectra vogelii Benth. is found in tropical and subtropical Africa. Climatic conditions are similar to those described for *Striga*, and in many cases the two are sympatric. Its range extends from South Africa throughout much of sub-Saharan Africa, threatening many crops (particularly peanut and cowpea). Evidence indicates that *A. vogelii* has developed host-specific strains, each attacking a narrow suite of hosts in southern and western Africa, but host specificity is more complex than that for *Striga* (7). Okonkwo and Raghavan (38) successfully conditioned *A. vogelii* seeds in 10 d at 25°C. The optimum day/night *temperatures* for germination and attachment were 25/15° and 30/20°C, respectively (36), well within the range of temperatures in its African habitats. Deviation in temperature from the optimum significantly reduced germination and attachment showing extreme sensitivity to extreme temperatures. Dawoud and Sauerborn (36) concluded that *A. vogelii* germination was significantly affected by conditioning period and osmotic potential, with low germination between −0.6 and −1.5 MPa at 5 d, suggesting sensitivity to drought, which could explain its restriction to savanna and its absence in semiarid regions (Fig. 4). *Aeginetia indica* is known to attack sugar cane in wet tropical areas of South Asia and Southeast

Asia. French and Sherman (39), studying the germination of *A. indica*, found that optimum temperatures for conditioning seeds were ≤20°C, with no germination in seeds conditioned at ≥25°C. Optimum germination temperatures were 25–30°C. The researchers also found an optimum pH of 5.9, and that light entirely inhibited seed germination.

Figure 4 summarizes known and predicted potential ranges of *Alectra vogelii* and *Aeginetia indica*. Neither species is known to occur outside its native range (primarily subtropical Africa and tropical and subtropical South Asia, respectively). However, model results indicate broad invasive potential extending to all continents (Fig. 4). In Africa, *A. indica* would be more restricted to wet tropical areas given the closer correspondence of climatic conditions to those in its native habitat in South Asia. Its broader invasive potential (compared with that of *A. vogelii*) in the Western Hemisphere could be due in part to its low temperature requirement for seed conditioning (Fig. 4). The work of French and Sherman (39) showed high germination in seeds conditioned at ≤20°C, and no germination in seeds conditioned at ≥25°C. The requisite low temperatures for conditioning could limit the ability of *A. indica* to grow successfully in the tropical and subtropical grassland where minimum summer temperatures exceed 25°C. Temperatures in wet tropical areas are within the optimum range for seed conditioning of *A. indica*, and as a result, this species has the potential to attack sugar cane and cereals in the tropics in both the eastern and western hemispheres.

A. vogelii is not predicted as a potential problem in wet tropical South America and South Asia, as is the case with most *Striga* species (Fig. 4), but it is more likely to be a problem across much of subtropical South America, the southeastern United States, Central America, subtropical southern Asia, and northeastern Australia, because the climatic conditions in those regions are similar to those of its native range. *A. vogelii* may present a real challenge to cowpea and peanut plantations in South Asia and to peanut and other Fabaceae in the southeastern United States and Central and South America where these crops are popular. Another species, *A. fluminensis*, is known to attack sugar cane in tropical and subtropical South America (4).

General Conclusions

Environmental factors were found to play major roles in determining geographic distributions of Orobanchaceae root parasites. These factors may act directly on germination, growth, and development of the parasite, or indirectly thorough host plants. For example, seeds of *Aeginetia*, *Striga,* and *Orobanche* are dormant and require a period of "after ripening" in warm, dry storage. In *Striga*, *Orobanche*, *Aeginetia,* and *Alectra*, this stage is followed by a period of conditioning (sometimes called preconditioning) in a warm and moist environment before the seeds can respond to germination stimulants produced by their hosts. Temperature and seed moisture content at the beginning of conditioning appear to play key roles in seed germination. For example, germination was 93 percent in seeds of *S. asiatica* stored at <10 percent moisture content, compared with 3 percent germination at 17 percent moisture content (40). The length of each period depends on environmental factors and varies among species. Germination in *S. hermonthica* is lower when conditioning was longer than necessary, which at 22°C, was 6 d (41). In addition, Orobanchaceae species have well-developed host-specific strains that can have different geographic ranges and require different treatments for germination. Light is found to inhibit seed germination and radicle expansion in most species, because seeds germinating on the surface have little chance of finding

host roots. Soil pH within the normal range of arable soils has little influence on the germination and development of Orobanchaceae, although alkalinity in soils may inhibit seed germination, because it has been shown to inactivate germination stimulants as in *S. hermonthica* (42). Day length does not seem to limit distributions of *Striga* and *Orobanche* (37).

Problems with parasitic weeds are compounded by many factors. For example, many regions in Africa and South Asia where these parasitic weeds are endemic are inhabited by small landholder farmers who are unable to adopt expensive chemical control or to use modern agricultural practices. Small farmers are also highly affected because of their dependence on precisely those crops hardest hit by these plants. In dry regions of the developing world, parasitic weeds take a large toll because of the limited number of crops that can be cultivated under these conditions. Other negative consequences of parasitic weed infestations include greater labor requirements, higher costs, greater risk of crop damage or yield reduction, and lower quantity and quality of produce.

Mack and Lonsdale (43) and Simberloff (44) concluded that it is difficult or impossible to eradicate invasive weeds once they become established. Eradication programs require significant commitments of labor and financial resources over long periods of time. For example, the United States Department of Agriculture and the state governments of North Carolina and South Carolina took more than 50 y and expended more than 250×10^6 to contain/eradicate *S. asiatica* (R. Eplee, pers. comm.; [45]). This expenditure was very much worthwhile compared to potential losses in corn production in this area and in the central portion of the country, if *Striga* were to spread to the Corn Belt. In the United States, crops threatened by witchweeds are valued at 20×10^9 annually, and crop losses from broad infestation by Orobanchaceae would clearly be in the hundreds of millions of dollars annually. Regardless of the benefit, many other countries may not be able to afford the costs of eradication or commit to such efforts for much time. Such countries would benefit from the adoption of less expensive alternative methods, which would minimize or prevent invasion of parasitic weeds to begin with.

The American experience is an excellent model for containment/eradication of parasitic weeds. The first step was recognition of the problem by the US Government, followed by passage of the Federal Noxious Weed Act to establish procedures for protection from devastating weeds of foreign origin such as *Striga*. These official steps were followed by *i)* extensive survey and mapping to determine areas infested; *ii)* regulatory activity, including establishment of quarantine measures to prevent spread to other areas, cleaning of equipment, commodities, and other materials before leaving infested areas; and *iii)* establishment of an eradication program, including the construction of research facilities in infested areas to develop methodologies for containment and eradication. Eradication was accomplished first by preventing growth, development, and reproduction of the parasite though mechanical, chemical, and cultural methods; and second, by devitalizing seeds in the soil via use of chemicals, seed stimulants, and false host crops. An excellent review of the problems of invasive weeds can be found in studies by Eplee (46) and by Veitch and Clout (47).

Good prediction systems provide the basis for successful management of invasive weeds. Many authors have realized the difficulties of eradicating invasive weeds, and have suggested means to prevent invasions and manage those invasive weed populations that become established. The first step in these programs is always a good prediction system that permits anticipation of the potential for invasions. In combination with prediction systems, early detection and management programs (for a comprehensive review see [48, 49]) should also be in place.

If prevention programs fail, limiting dispersal is a fundamental strategy in invasive species control. In certain situations, containment of incipient invasive populations may be an important management technique.

The ecological niche modeling approaches used herein provide a quantitative, predictive basis for anticipating the geographic potential for species' invasions. Because of their basis on ecological niche characteristics, these models allow for anticipation of a broad suite of biodiversity phenomena, including effects of climate change and habitat alteration on invasive potential (22), effects of land use on species' distributions, and effects of biotic interactions in modifying species' potential distributions (14). Effects of parasitic weeds on agricultural production may increase when agricultural systems become more vulnerable to the parasite owing to climate change, which may be true for many areas that are now free of Orobanchaceae parasitic weeds.

In addition to the experience described above in the United States, we suggest six steps:

i) Establish and enforce quarantine and eradication programs to minimize the spread of parasitic weeds within and between regions. Some countries such as Australia, Canada, India, Iran, Malaysia, Russia, and the United States already have this measure in place.

ii) Establish state and regional offices to deal with and coordinate control and containment programs, which could be part of state departments of agriculture or organizations similar to the European and Mediterranean. Plant Protection Organization and European Cooperation in scientific and technical research and its affiliate organization, Parasitic Plant Management in Sustainable Agriculture.

iii) Map areas infested by parasitic weeds that may affect agricultural crops in detail—techniques such as those illustrated herein make possible a quantitative and predictive understanding of distributions of each species in key groups of pest weeds, and can indicate regions of likely spread.

iv) Develop parasitic weed management polices and programs to share knowledge regarding parasitic plants.

v) Develop educational programs to alert and educate the public about the dangers of these weeds to agricultural systems.

vi) Establish an international office to coordinate the global work on parasitic plants.

Coming steps in the development of our approach to enriching geographic information about parasitic weeds will include the issue of including information on host distributions in the ecological niche models of the parasites. Although the potentially broad host range of these parasites will make this step a considerable challenge, host distributions clearly can enrich the quality and predictability of the models. Also, we will include issues of global climate change and how it will likely modify the invasive potential of parasitic weed species—tools for developing such projections are already well developed for applications to biodiversity conservation (50), and adaptation for application to parasitic weeds should be straightforward. These two steps can greatly enrich the information expressed in these modeling efforts.

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