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Geographical distribution and aspects of the ecology of the hemiparasitic angiosperm *Striga asiatica* (L.) Kuntze: a herbarium study

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ABSTRACT. *Striga asiatica* (Scrophulariaceae) is an obligate root hemiparasite of mainly C_4 grasses (including cereals). It is the most widespread of the 42 *Striga* species occurring in many semi-tropical, semi-arid regions of mainly the Old World. Examination of herbaria specimens revealed that *S. asiatica* has a wider geographical distribution, is present at higher altitudes and occurs in a more diverse range of habitats than previously reported. The host range is also larger than previously reported and is likely to include a large number of C_3 plants. Morphology of examined specimens revealed variation in size and corolla colour suggesting the existence of ecotypes. Climate may exert a significant influence on the distribution of *S. asiatica* given the diversity of potential host plants and their distribution beyond the current recorded range of *S. asiatica*.

KEY WORDS: distribution, ecology, host range, *Striga asiatica*

INTRODUCTION

Striga is a genus of 42 currently described species (Aweke 1992, Barker 1990, Raynal-Roques 1991;) of obligate root hemiparasites in the Scrophulariaceae, most of which are annuals. They are native to semi-arid, semi-tropical areas of the Old World and two species have been accidentally introduced to parts of the United States (Sauerborn 1991). Eleven species are regarded as agricultural weeds, of which four can be serious economic pests (*S. hermonthica*, *S. asiatica*, *S. aspera* and *S. gesnerioidies*)(Raynal-Roques 1991). The hosts of most *Striga* species are grasses including the C_4 cereals maize, millet, sorghum and sugar cane and the C_3 cereal upland rice (Musselman 1980).

All *Striga* species are chlorophyllous, erect plants with small (up to 2 cm long) leaves and terminal flower spikes. Each plant produces large numbers (between 25,000 and 200,000) of tiny (length 0.33 mm, weight 3.7 μg) seeds (Parker & Riches 1993), which have a longevity of between 10 and 20 y in the soil seed bank (Bebawi *et al.* 1984, Saunders 1933). The life cycle of the parasite

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is intimately linked to that of its host by a series of chemical cues, and to the climate, particularly during post-ripening and pre-conditioning phases (e.g. Musselman 1980). Seed germination requires a specific chemical signal present in host root exudate, and a second chemical signal is then required to induce the formation of the primary haustorium (see Boone *et al.* 1995 and Riopel & Timko 1995 for recent reviews). Subsequently a large number (tens to hundreds) of secondary haustoria are formed. Once the parasite has penetrated the host root, there appear to be additional signals which may determine whether or not the host-parasite association will be compatible, since in some associations, parasites which have germinated and started to penetrate host root tissue become arrested and subsequently die (Lane *et al.* 1993). Thus there are a series of windows which control host specificity for the genus.

Striga has pronounced effects on host growth and yield, which are substantially reduced (Press *et al.* 1991), and the effects of *Striga* can be severe even before emergence of the parasite above ground (Ramaiah & Parker 1982). Quantification of the effects of *Striga* is difficult because of the influence of environmental factors of the host-parasite interaction.

S. asiatica is, geographically, the most widespread of *Striga* species; large populations having been reported throughout sub-Saharan Africa, South-East China and the Indian sub-continent while smaller, isolated populations have been reported in Arabia, Indonesia, Philippines, North and South Carolina (U.S.A.) and Australia (Musselman 1980, Sauerborn 1991). The presence of *Striga* is estimated to extend to 40% of arable land in sub-Saharan Africa and to 67% of savanna zones under cereal production (Lagoke *et al.* 1991, Mboob 1989).

S. asiatica is known to occur widely in savanna grasslands but at much lower densities than observed in agricultural systems (Raynal-Roques 1987). A number of authors have identified native hosts of the parasite (Hosmani 1978, Kumar & Solomon 1941, Nelson 1958, Sand 1987) but little work has focused on the relationships between *S. asiatica* and its native hosts in these natural ecosystems except in the United States following the discovery of *S. asiatica* in the 1950s (Sand *et al.* 1990).

This paper aims to use herbaria specimens to: (i) identify the geographical range of *S. asiatica*, (ii) investigate the morphological variability of the species, (iii) identify potential hosts, (iv) identify habitat range, and (v) compare the information obtained with published literature.

Information on the range of natural hosts of *S. asiatica* will provide the basis for further investigation of the interactions between the parasite and its native hosts in natural ecosystems.

APPROACH

Collections of *S. asiatica* from European herbaria were examined (Table 1). A total of 2277 specimens were examined and details of location, altitude, corolla

Table 1. List of herbaria from which specimens were examined. The numbers of specimens examined at each location are given.

Herbarium	Number of specimens
Museum National d'Histoire Naturelle, Paris, France	849
Royal Botanic Gardens, Kew, U.K.	691
Rijksherbarium, Leiden, Netherlands	422
Natural History Museum, London, U.K.	203
Royal Botanic Garden, Edinburgh, U.K.	100
Dept. Plant & Soil Science, University of Aberdeen, U.K.	6
National Museums & Galleries, Liverpool, U.K.	6

colour, plant height, branching pattern, habitat and associated vegetation, soil type and host species were recorded when accompanying information was available.

RESULTS

Geographical range

Specimens examined were collected between latitudes 31°N and 28°S and longitudes 14°W and 150°E in Africa and Asia, respectively. The specimens from the United States were from approximately latitude 35°N, longitude 80°W. *S. asiatica* specimens were collected from 67 different countries (Figures 1a,b) although not all sheets provided enough detailed information to plot locations accurately (*c.* 70% were plotted). It is likely that *S. asiatica* also occurs in countries adjacent to those marked where climate and vegetation are similar but where collection of specimens has not been possible because of political or other reasons (e.g. in Laos and Namibia).

The list of countries from which examined specimens has been collected is in general agreement with lists in published literature although a number of countries, states or islands not previously recorded within the range for *S. asiatica* were described. It is not possible to ascertain from the available information whether these discrepancies are due to lack of information available to earlier authors. No specimens were available to support recent reports of *S. asiatica* in the Nile delta region of Egypt (Zahran & Willis 1992). This may indicate that *S. asiatica* is currently undergoing an expansion in its distribution.

Ecological range

Specimens were collected from a range of altitudes from sea level to 2750 m a.s.l. (Figure 2), 4.4% of specimens had detailed information of the collection site being over 2000 m a.s.l. although most of the specimens collected from Yemen and Saudi Arabia (28) and the Himalayan region (68) are also likely to be from high altitude sites. Information attached to a number of specimens described the collection site as being mountainous or hilly although no altitude was given. Agnew & Agnew (1994) describe the range of *S. asiatica* as being from sea level to 2480 m. Most accounts of *S. asiatica* describe its habitat range

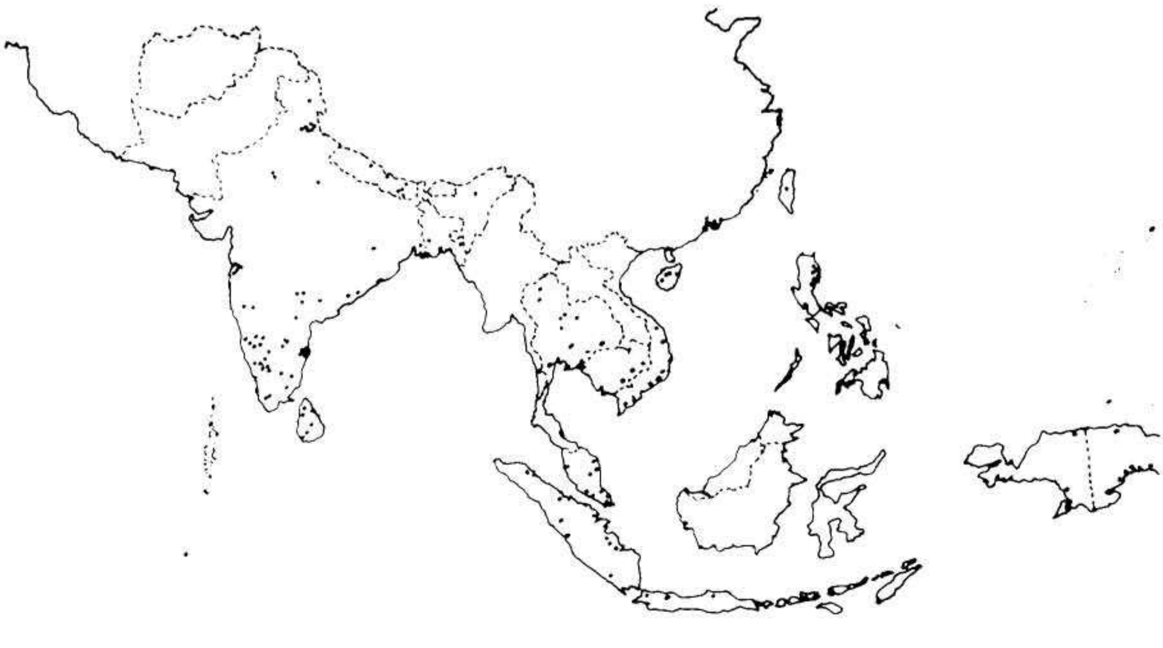

Figure 1. Maps of (a) Africa and Arabia, and (b) S.E. Asia, Indian Ocean Islands and Indian sub-continent, showing collection points of *S. asiatica* specimens examined. • represents collection sites.

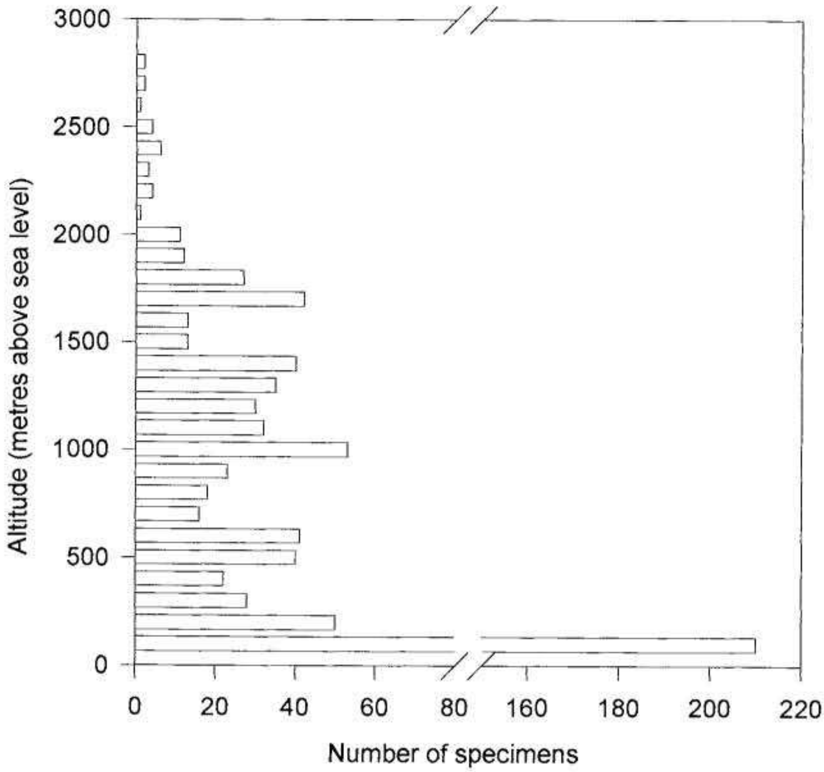

Figure 2. The altitudinal distribution of 781 *S. asiatica* specimens examined.

as semi-arid and semi-tropical (e.g. Kasasian 1971, Musselman 1987, Parker & Riches 1993) and its presence at high altitudes would indicate that the species is more widely distributed than previously thought. Patterson (1990) has shown that *S. asiatica* is more tolerant of low temperatures than other *Striga* species, with the seeds retaining viability after periods of storage at −7° C and the plants being able to reach maturity at a daily mean temperature of 22° C, although the optimum temperature for growth is approximately 30° C.

Over half (61%) of the specimens were collected from savanna or grassland and 15% from, or close to, cultivated land. The remaining specimens were collected from a diverse range of habitats not normally regarded as areas suitable for the growth of *S. asiatica* (Table 2), although Raynal-Roques (1987) reports that the species occurs on soils which are sometimes temporarily waterlogged.

Where soil type was described (470 records) most were shallow, sandy, rocky or lateritic. These are likely to be low nutrient, dry soils which are known to favour the growth of *Striga* species. The addition of fertiliser (particularly nitrogen) to soils has been shown to reduce the incidence and effects of *Striga* on agricultural hosts under field conditions (Guled *et al.* 1991, Okafor & Zitta 1991, Osman *et al.* 1991). There were, however, a number of reports of *S.*

Table 2. Descriptions of habitat types from which *Striga asiatica* was collected as described on examined herbaria sheets.

Habitat type	No. of records
Savanna/grassland	565
Wooded savanna/scrubland	72
Cultivated areas	137
Woodland/forest	66
Bare ground	17
Grazed pasture	28
Marshes/swamps	26
Pools/ponds	15

asiatica occurring on black (humus rich), clay, wet and alluvial soils which have a higher nutrient status and are not normally associated with the parasite.

Morphology

The morphological range of *S. asiatica* was extensive in terms of overall plant height, extent of branching and corolla colour. It has been generally accepted that corolla colour is usually specific to a region: red in Africa and white in Asia and the United States (Musselman 1987, Parker & Riches 1993, Raynal-Roques 1987). Table 3 shows that although this is generally true the variation within geographic regions is large. The only two specimens available from the United States were both described as having scarlet flowers although Patterson (see Sand *et al.* 1990) reports that *S. asiatica* seen in the country had white corollas and displayed little genetic variation.

Information on the overall height and extent of branching of the specimens examined is shown in Table 4. Published descriptions of *S. asiatica* (e.g. Musselman in Sand *et al.* 1990, and Parker & Riches 1993) describe the plant as being up to 30 cm tall. Most (93%) of the specimens examined were between

Table 3. Corolla colour of *S. asiatica* in different regions of the world as taken from herbaria sheet information. Values are numbers of specimens examined, and figures in parentheses refer to the percentage of specimens in that region only.

	Corolla colour						
Region	Red	Yellow	White	Pink	Purple	Orange	Total no. of specimens
Africa	964 (80.6)	167 (14.0)	23 (1.9)	14 (1.2)	2 (0.2)	26 (2.1)	1196
Indian subcontinent	15 (12.1)	13 (10.5)	94 (75.8)	2 (1.6)			124
Asia	58 (16.4)	201 (56.9)	82 (23.3)	4 (1.1)			353
Arabia	38 (67.8)	10 (17.9)	8 (14.3)				56
Indian Ocean Islands	68 (29.4)	125 (54.2)	22 (9.5)	13 (5.6)	3 (1.3)		231
USA	2 (100)						2
Australia	1 (50)	1 (50)					2

Table 4. Overall plant height and extent of branching in specimens of *S. asiatica* examined in this study. Values given are numbers of specimens, and figures in parentheses refer to percentages within each height group.

Ht (cm)	No branches (0)	Few branches (1–10)	Many branches (>10)	Total no. of specimens
4–10	266 (66.7)	127 (31.8)	6 (1.5)	399
11–20	546 (54.3)	384 (38.2)	75 (7.5)	1005
21–30	261 (44.5)	217 (37.1)	108 (18.4)	586
31–40	57 (52.7)	41 (32.0)	30 (23.3)	128
41–50	4 (21.1)	7 (36.8)	8 (42.1)	19

4 and 30 cm yet the remaining 7% were between 31 and 50 cm in total height. Where habitat information was provided it seems that the majority of tall and highly branched specimens were collected from the vicinity of agricultural areas, indicating that host type is a major factor in determining vigour and growth of the parasites, although the existence of a number of different ecotypes of *S. asiatica* cannot be ruled out.

Host range

Although only 68 of the specimen sheets examined provided details of potential or putative native hosts (Table 5) (a further 68 were reported as growing on cultivated hosts) ten of the genera identified have not previously been reported as hosts of *S. asiatica*. Within genera which have been previously cited as hosts 17 species described in this study have not been listed elsewhere. All genera described as hosts have a wide geographic range. For example: *Digitaria*, *Cynodon* and *Chrysopogon* occur outside the current range of *S. asiatica* in warm temperate regions of Asia and Australia; *Elionurus*, *Eleusine*, *Eragrostis* and *Loudetia* also occur widely in South America and *Hyparrhenia* also occurs in the Mediterranean region (Clayton & Renvoize 1986) and there is no apparent division between host species and region.

Of 93 previously reported non-agricultural graminaceous host species of *S. asiatica* all are C_4 plants except for *Agropyron cristatum*, *A. repens*, *A. trichophorum*, *Agrostis alba*, *Avena fatua*, *A. sativa*, *Bromus inermis*, *B. tectorum*, *Dactylis glomerata*, *Hordeum intermedium*, *Poa annua*, *P. pratensis*, *P. trivialis*, *Secale cereale* and *Triticum vulgare* (Hosmani 1978, Kumar & Solomon 1941, Nelson 1958, Sand 1987).

Grasses growing at high altitudes are unlikely to possess the C_4 photosynthetic pathway. For example, there is a very sharp transition zone between the presence of the two photosynthetic pathways in grasses at around 2000 m in upland Kenya (Tieszen *et al.* 1979). The hosts of the 34 specimens found at altitudes above 2000 m are, therefore, likely to be C_3 species. With the exception of rice, all hosts identified in this study were C_4 grasses. The highest altitude at which a host was identified was 1600 m.

Hosmani (1978) and Kumar & Solomon (1941) both list a number of hosts for *S. asiatica* which are not grasses. These hosts are mainly legumes but also include ten other families. No recent work has confirmed these reports and

Table 5. List of non-agricultural hosts and country in which reported of *Striga asiatica* from herbaria sheets. A total of 68 specimen sheets provided details of non-agricultural host species.
Previous references: 1. Hosmani (1978), 2. Kumar & Solomon (1941), 3. Sand (1987), 4. Nelson (1958), 5. Visser (1981), 6. Sherif *et al.* (1987), 7. McGrath *et al.* (1957), 8. Moreno & Cubero (1996).

Host species	Countries in which reported	Previous reference as host
Andropogon spp.	Nigeria, Tanzania, Uganda, Zambia, Zimbabwe	1,2,3,4,5
Andropogon gayanus	Ivory Coast	
Brachiaria deflexa	Tanzania	5
Brachiaria umbellata (Panicum umbellata)	Seychelles	
Chrysopogon sp.	Yemen	
Cymbopogon sp.	Tanzania	
Cynodon spp.	S.W. Arabia, Zambia	1,2,3,5,8
Dactyloctenium sp.	Kenya	3,8
Dactyloctenium giganteum	Tanzania	
Digitaria spp.	Mafia Island, Malawi, Tanzania, Zambia	1,2,3,5,8
Digitaria gayana	Nigeria	
Digitaria abyssinica (D. scalarum)	Tanzania	
Diheteropogon amplectens	Tanzania	
Eleusine coracana	India	1,2,7
Eleusine indica	Ethiopia	3,4,6,8
Elionurus elegans	Mali	
Eragrostis sp.	Tanzania	1,2,3,4,5,7
Eragrostis subaequiglumis	Aldabra Island	
Eragrostis superba	Tanzania	
Exotheca sp.	Tanzania	
Heteropogon sp.	Zimbabwe	
Heteropogon contortus	Tanzania	
Hyparrhenia spp.	Malawi, Tanzania, Uganda	
Loudetia spp.	Cameroon, Malawi, Zambia	
Loudetia kagerensis	Cameroon	
Microchloa sp.	Ghana	
Panicum coloratum	Tanzania	1,2,7
Panicum maximum	Mozambique, Togo	1,2,7
Paspalum spp.	Sumatra	8
Pennisetum purpureum	Malawi	
Rhynchelytrum repens	Tanzania	
Setaria sp.	Cameroon, Sudan	1,2,3,4,5
Setaria incrassata (S. phleoides)	Zambia	7
Sorghum (wild)	Malawi	1,3,4
Sorghum versicolor	Tanzania	1
Sporobolus sp.	Zambia	1,2,5
Sporobolus festivus	Tanzania	
Sporobolus pyramidalis	Tanzania	
Themeda sp.	Zimbabwe	
Themeda triandra	Tanzania	
Urochloa sp.	Tanzania	2,5
Urochloa trichopus	Tanzania	

no evidence from the herbaria specimens examined in this study was found to suggest that *S. asiatica* will parasitise non-graminaceous species. Some of the hosts listed by Hosmani are referred to as false hosts by Musselman (1987), exudate from roots of these species will induce germination of *Striga* seeds but these are then unable to attach or form a haustorium.

Conclusion

The information presented here demonstrates that both the host range and the geographic range of *S. asiatica* is greater than previously thought. In particular, the plant appears to be present at higher altitudes than reported previously. This implies that its host range will also include a large number of C_3 grasses. Although the life cycle of *S. asiatica* is closely linked with its host, through chemical cues which control parasite development, it seems that a large number of grasses with wide distributions are potential hosts.

The large morphological variability seen in the specimens may indicate the presence of ecotypes and requires further investigation.

Climate may impose restrictions on the distribution of the species through host availability and any global environmental changes which alter the range of host species will also affect the distribution of the parasite. The tolerance of *Striga asiatica* to a relatively wide range of environmental factors may allow it to expand its range along with its hosts. The implications of any extension would not only be ecologically important but could also be important for agriculture.

This study reveals gaps in our understanding of the ecology of *S. asiatica* and it is clear that more work (in particular field studies) are essential if this important species is to be better understood. The study does, however, provide information which will allow laboratory investigations into native host-parasite associations to be conducted.

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