

COMPARATIVE STUDIES ON THE COMPETITIVE ABILITIES OF AN EXOTIC, *PARTHENIUM HYSTEROPHORUS* L., WITH CO-EXISTING SPECIES TO DETERMINE THE IMPACTS OF ITS INVASION

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Abstract

Germination percentage of a newly introduced exotic plant, *Parthenium hysterophorus* L., that has now dominated most of the herbaceous flora, was compared with 7 annual indigenous colonizer plants, commonly found in the wastelands of Lahore, Pakistan. The percentage of germination, determined under various sets of conditions revealed that having higher and relatively constant rates of germination throughout the year, *P. hysterophorus* is more competitive as compared to the other co-existing colonizers. The competitive abilities of *P. hysterophorus* were further compared with two dominant colonizers i.e., *Chenopodium album* and *Kochia indica*, to assess the competitive abilities on both interspecific and intraspecific competition. The results based on Absolute Yield, Relative Yield Total and Relative Crowding Coefficients clearly indicated that *P. hysterophorus* was competitively more aggressive as compared to both co-occurring species and there is a possibility that in the long run it would eliminate them from their habitat in the irrigated plains.

Introduction

Parthenium hysterophorus L., a native of Mexico and Central America (Navie *et al.*, 1996) is one of the 10 worst weeds in the world (Oudhia, 2002) and in Western Australia it has been declared noxious weed of category A –eradication (Navie *et al.*, 1996). Previous studies reported herbaceous annual species that dominate the wastelands of Lahore, Pakistan, without any reference of *Parthenium hysterophorus* (Khan & Rizwanullah, 1988). Its introduction in the Indian Sub-continent can be traced back to 1955 as an escaped one, from the Indian state, Poona, where it was introduced accidentally as a contamination in the wheat consignment from America (Labrada, 1988; Oudhia, 2001). This annual exotic plant is a recent introduction in Pakistan being noticed in small numbers in the suburbs of Lahore in the early 1990's (Meraj, 1998). Presently it has invaded most of the wastelands in the suburbs of Lahore and a survey of the area reveals that the common species, viz., *Abutilon indicum*, *Acyranthes aspera*, *Cassia occidentalis*, *Chenopodium album*, *Croton sparsiflorus*, *Kochia indica* and *Withania somnifera* are being suppressed by *Parthenium hysterophorus* (Vehra, 2002). Since the biggest damage from exotic plants is homogenization of biota (McNeely, 1998), it is therefore imperative to study the viability of seeds under various sets of conditions ensuring its survival as compared to other associated annual species. Additionally, experiments with codominant species were undertaken to study the competitive aspects of its invasion.

Previous investigations (Kjellssar, 1997), suggested that viability of seeds could most conclusively be evaluated on the basis of germination. Ricardo & Velasco (1987) used the fruit pulp of *Arbutus unedo* to study inhibitory effect, if any, on its germination. Karagulzel *et al.*, (2004) subjected seeds of *Lupinus varius* L., to various seed coat treatments to study their effects on germination and early seedling growth. Different range of experimental conditions from Petri dishes to sterile sand cultures (Garg & Garg, 1982; Nasrini & Rahman, 2007) have been used to test the viability of seeds. Previous findings regarding germination characteristics of *P. hysterophorus* are controversial and need to be explored further as on one hand Navie *et al.*, (1998) reported initial inhibition of germination in freshly

shed seeds and suggested seed incorporation into the soil to be important to the long term persistence of *P. hysterophorus* seeds and on the other hand McFadyen (1992) reported absence of a primary dormancy mechanism in the seeds of *P. hysterophorus*.

Many studies on inter- and intra-specific competition between species have been carried out, by using Replacement Series Experiment and Space Occupation Experiment (de Wit, 1960). For instance, Jolliffe *et al.*, (1984) concluded that barnyard grass (*Echinochloa crusgalli*) was more competitive than green foxtail (*Setaria viridis*). Similarly, Martin & Field (1987), studied competition between vegetative plants of wild oat (*Avena fatua* L.) and wheat (*Triticum aestivum* L.) using replacement series model and concluded that wild oat was more competitive than wheat. Khan & Morton (1994), made a comparative study on the growth strategies in two varieties of *Arrhenatherum elatius* - and wheat, whereby intraspecific competition was studied using β - parameter and the results clearly indicated that wheat suppressed Onion Couch more than the Tall Oat grass and that the latter variety was more aggressive than the former. Fetene (2003) used Replacement Series to evaluate the influence of perennial grass (*Hyparrhenia hirta*) on the establishment of tree (*Acacia etbaica*) seedlings and found that the perennial grass was competitively aggressive towards seedlings of the tree.

The present research work is an effort to relate viability in terms of high percentage of germination capability of the exotic and co-existing species in the context of early establishment and hence higher competitive ability as well as to interpret the nature of competition, if any, between *P. hysterophorus* and dominant colonizer species in order to predict the impact of the exotic species on the diversity of the landscape.

Materials and Methods

The present study was carried out in two parts. The first part was concerned with the viability of seeds of (*P. hysterophorus* and seven co-occurring plant species), based on germination experiments under different sets of

conditions. The most competitive species, screened on the basis of this experiment were then used in the second experiment for analyzing their competitive abilities.

Site of experiment: The field experiments were carried out at the Government College Botanic Gardens (GCBG), Lahore, Pakistan, whereas the germination experiments were set up in the laboratory in the Botany Department, Government College University, Lahore.

Collection of seeds: Since *P. hysterophorus* is an annual species so along with it, seeds of 7 other co-existing summer annual species were collected from the wastelands in the suburbs of District Lahore, Pakistan, from September to November 2001, for both germination and competition experiments. The seeds were stored in paper bags at room temperature.

a. Assessment of seed viability: Assessments for seed viability, based on percentage of germination were made, each day for a period of one week after sowing. Plumule emergence was the criterion used to determine initiation of germination. The viability of seeds was checked under four laboratory and one field experimental conditions and were run in the first week of each month, from February 2002 to September 2002. The average room temperature was 23.5°C during the period of experiment from February to September. The light and dark period to which the seeds were exposed corresponded to the natural day and night length, the average intensity of day light being 80 Lux (Lux light meter, 726693, TENMA). The following experiments were set up in three replicates in the laboratory:

1. Germination of seeds- only in Petri plates: Twenty seeds of each of the eight plant species were sown in Petriplates (9 cm diameter), on 4 cellulose (Whatman No.1) filter papers, moistened with 50 ml of distilled water at room temperature. To prevent contamination with microbial growth, the Petriplates along with moistened filter papers were autoclaved at 121°C at 15 psi for 15 minutes, and then allowed to cool at room temperature, prior to placing seeds on them.

2. Germination of seeds with fruit pulp in Petri plates: Germination tests for seeds with fruit pulp were prepared by removing the seeds (of each species separately) from the fruit and grinding the remaining parts of the fruits in a mortar and pestle, with 50 ml of distilled water. After placing the 20 seeds per Petri plate, the paste of its own fruit pulp was poured over it and the petriplates were shaken gently, to spread the fruit pulp evenly over the seeds and were kept at room temperature.

3. Germination of seeds in sand culture: Twenty seeds of each species were sown (at equidistant points), in separate trays (25 x 20 cm), containing heat sterilized (at 105°C for 24 hours) sand (500 cm³), which was presoaked with 50 ml of distilled water. The experiment consisted of randomized block design. The trays were placed at room temperature and watered when required.

4. Germination experiment in germination chambers: In addition to the germination experiments carried out in the

above-mentioned three conditions, percentage germination was also determined, using germination chambers.

Controlled conditions of temperature and relative humidity were maintained in the germination chambers. A range of temperature of 25°C to 27°C and relative humidity 40 to 43%, was chosen, as this corresponded to the average, temperature and relative humidity prevailing during the months of March and April, when germination of most of the summer annuals commences in the natural conditions.

The experiment was run in triplicates for each species, using 50 seeds per species per sample. Observations were made one week after initiation (7th January 2002) of the experiment.

Germination experiment under natural field conditions: A germination experiment was also carried out in natural conditions in the Government College, Botanic Garden. Plots (0.5m²) were marked and 50 seeds per plot were sown for each species, in triplicates. The plots were watered when required and observations were made on daily basis for three weeks. The experiment was set on 10th February 2002, which corresponds with the beginning of spring period.

b. Assessment of competitive ability: In order to analyze the competitive abilities of the species the following experiments were planned: Replacement Series Experiment developed by de Wit (1960), to study inter-specific competition (Baeumer & de Wit, 1968) and Space occupation Experiment (de Wit, 1960) to study intra-specific competition.

Two sites of 75m² and 95 m² were selected for 'Replacement Series Experiment' and 'Space Occupation Experiment', respectively. In order to obtain statistically valid results, randomized complete block design was selected. The experiment was initiated in April and terminated in mid-August 2002.

Design of replacement series experiment: In the replacement series experiments plant species are grown in monocultures and in mixtures, in varied proportions, but at constant overall density.

The Replacement Series was designed into two adjacent blocks (each in three replicates) one for *Chenopodium album* and *Parthenium hysterophorus* and the other for *Kochia indica* and *Parthenium hysterophorus*. As each series consisted of 7 different combinations, 7 plots each 1 m² were arranged in a row, but with 0.25 m wide strip of land between each plot. The proportion of plants in each series was 12:0, 10:2, 8:4, 6:6, 4:8, 2:10 and 0:12 with the corresponding relative planting frequencies being 1/0, 0.83/0.17, 0.67/0.33, 0.5/0.5, 0.33/0.67, 0.17/0.83 and 0/1.

Estimation of interspecific competitive ability: The interspecific competitive ability was estimated on the bases of the following parameters:

1. Root/shoot ratio (dry weight)
2. Relative yield and relative yield total
3. Relative crowding coefficient
4. Replacement diagrams based on the yields of each species plotted against the relative planting frequencies of species

Design for 'space occupation experiment': Seeds of *P. hysterophorus*, *C. album* and *K. indica* were sown in monoculture at low planting density (20 plants) and high planting density (200 plants). For each species 30 plots of 1m² (to provide for 5 monthly harvests in triplicate) were laid out separated by 0.25m wide path on all sides. After each harvest, plants were dried in oven at 100° C for 24 hours.

Estimation of intraspecific competitive ability: Estimation of intraspecific competitive ability was made on the basis of trends in 'Parameter β', represented graphically in the form of β-Curve (de Wit, 1960), that in turn represents the space occupied by a single plant.

Harvest: Analysis for the Replacement Series experiment was based on assessment made by a single destructive harvest carried out in mid –August 2002. The results were based on oven dry weight (100°C for 24 hrs) of shoots, roots and whole plants.

For Space Occupation Experiment, five destructive harvests, in triplicates, were carried out for each species at monthly intervals commencing from April 2002 to August 2002 and their dry weights were recorded.

Statistical analysis: The statistical analysis carried out involved calculation of Standard Error (Steel & Torrie, 1960).

Results

a. Seed viability: Germination experiments on viability of seeds of 8 different plant species of the wastelands of Lahore, Pakistan, under different experimental setup are described. The germination percentage (Fig. 1) obtained from the experiment conducted in germination chambers showed maximum values for *K. indica*, followed by *P. hysterophorus* and *C. album*, and were found to be consistent throughout the study period. The same pattern was observed for experiment carried out under natural conditions in the field.

In the experimental setup on filter paper, in Petri plates (Fig. 2) the three species showing consistently highest germination rates, in the descending order, were *K. indica* (88.34%), *P. hysterophorus* (71.67%), and *C. album* (70%). A dramatic and sudden drop was observed in the germination percentage values for *K. indica* and *C. album* in August and September. However, no such change was recorded for *P. hysterophorus*, as its germination results remained fairly constant throughout the experimental period. During March, a rise in germination percentage was registered for all the species. However, the germination rates for *A. indicum* (0-20%), *A. aspera* (1.67-30%), *C. occidentalis* (3.34-21.67%), *C. sparsiflorus* (6.67- 26.67%) and *W. somnifera* (0-3.34%) remained relatively low throughout.

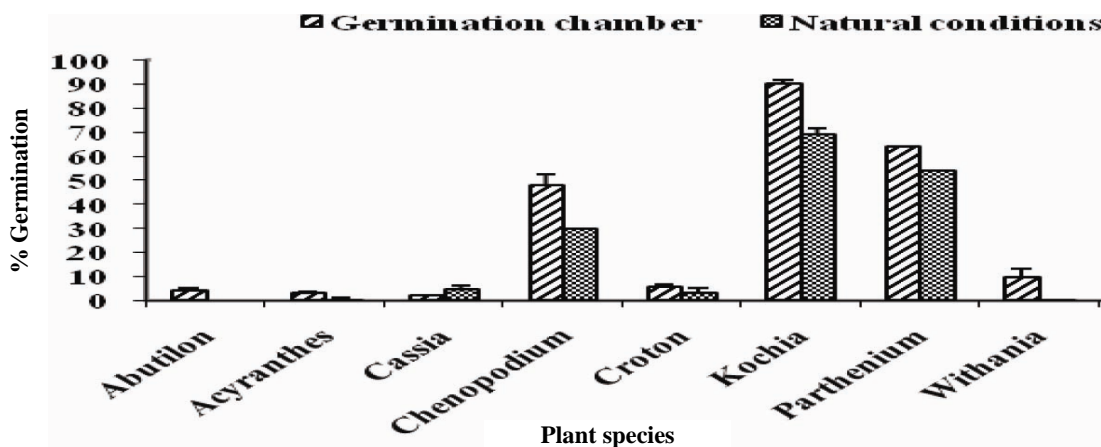


Fig. 1. Percentage germination in germination chambers and in natural field conditions.

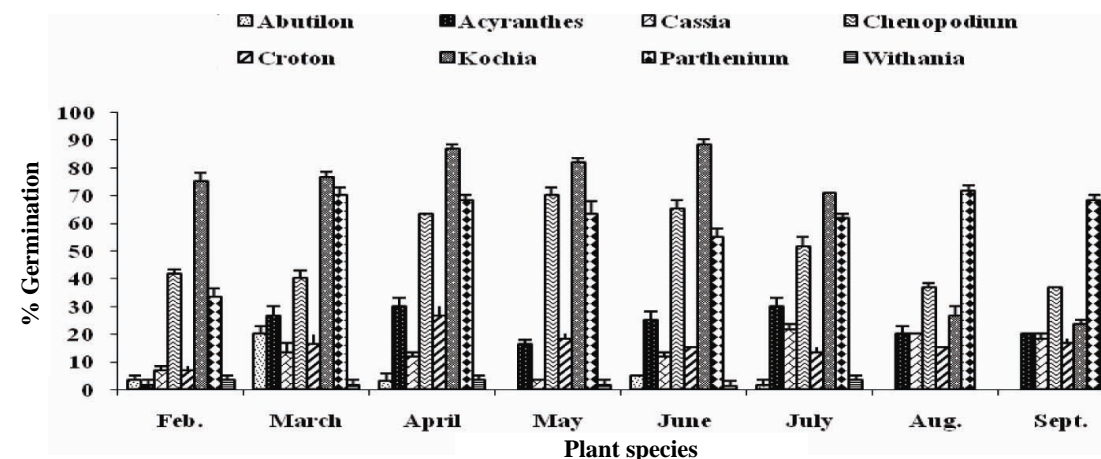


Fig. 2. Germination percentage of seeds on filter paper, without fruit pulp.

In the other experimental setup with seeds on filter paper, with the addition of fruit pulp (Fig. 3), it was found that germination in *C. album* was most affected by the presence of fruit pulp as it showed a decrease in germination rates throughout the experimental period, followed by *A. aspera*, *C. occidentalis*, *K. indica* and *W. somnifera*. While *P. hysterophorus* and *A. indicum* showed a varied response, seed viability in *C.*

sparsiflorum, *P. hysterophorus* and *A. indicum* was not much affected by the presence of fruit pulp.

The results for germination percentage of seeds in sterile sand culture (Fig. 4) depicted a general increase over those on filterpaper, for *C. sparsiflorum*, *A. aspera*, *C. occidentalis* and *C. album* while *A. indicum*, *K. indica*, *P. hysterophorus* and *W. somnifera* showed a varied response.

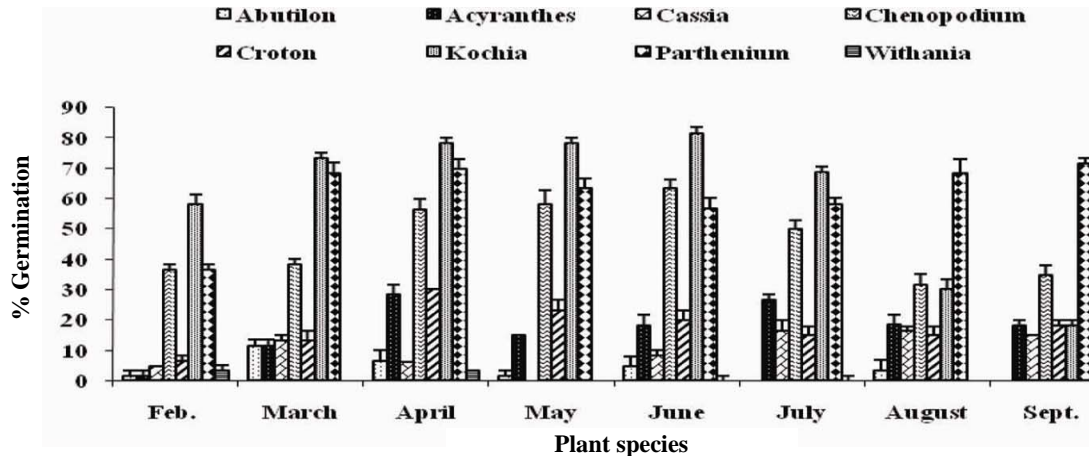


Fig. 3. Germination percentage of seeds on filter paper with fruit pulp.

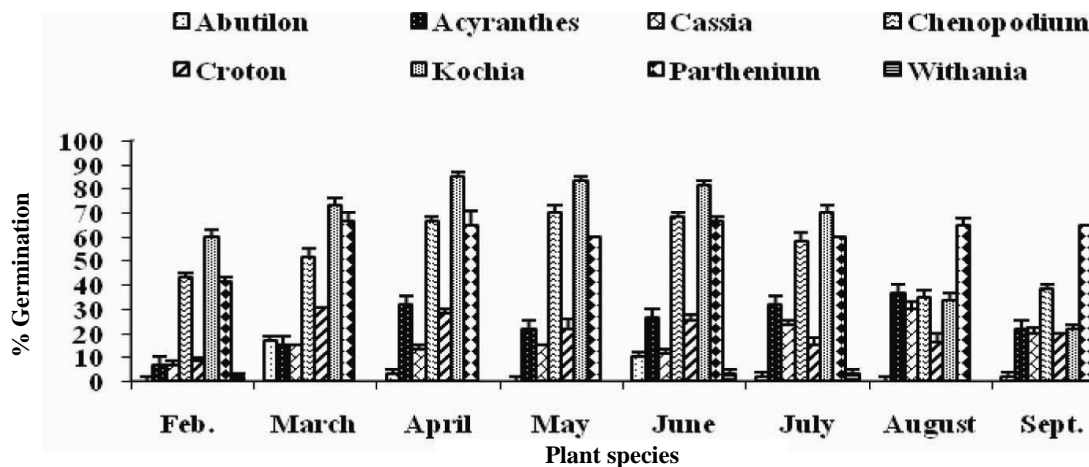


Fig. 4. Germination percentage of seeds in sand.

b. Competitive abilities

Interspecific competition: In Replacement Series Experiment, the root/shoot ratios of *C. album*, *K. indica* and *P. hysterophorus* for all the three plants were low, being less than one, showing that the plants directed more energy towards shoot than roots (Table 1) The comparatively higher values for *P. hysterophorus*, indicated that the plant directed relatively more energy towards the root than *C. album* and *K. indica*.

The relative yield total (RYT) for *C. album* vs. *P. hysterophorus* and *K. indica* vs. *P. hysterophorus* was found to be unity (Figs. 5&6), or nearly so, and it could be deduced that both *C. album* and *K. indica* were competitive with *P. hysterophorus* and were crowding in the same 'space', thus making demands on the same limiting resources.

The product of relative crowding coefficients, in all but two planting frequencies is higher than one (Table 2), indicating a competitive relationship between the local dominant and exotic species. Overall, *P. hysterophorus* proved to be more aggressive than the other two species, as indicated by higher Relative Crowding Coefficient values.

The replacement diagrams (Figs. 7&8) show that the 'actual' yields of both the species deviate from the 'expected' yields. Interestingly, *P. hysterophorus* exceeded its 'expected yield' whereas both *C. album* and *K. indica* did not attain it, thus it is clearly indicative of a competition between the exotic and the native species, the competition being of the 'compensatory' type, in which *P. hysterophorus* appears to be a better competitor. Moreover, relatively earlier decline of the graph line for *C. album* as compared to *K. indica* suggested that *P. hysterophorus* competed with *C. album* more strongly than with *K. indica*.

Table 1. Root/shoot ratio of dry weights of *C. album* vs. *P. hysterothorus* and *K. indica* vs. *P. hysterothorus* in replacement series experiment.

Relative planting frequencies	Root: Shoot		
	<i>C. album</i>	<i>P. hysterothorus</i>	
<i>C. album</i> vs. <i>P. hysterothorus</i>	1/0	0.095	-
	0.83/0.17	0.055	0.130
	0.67/0.33	0.064	0.100
	0.5/0.5	0.078	0.134
	0.33/0.67	0.087	0.086
	0.17/0.83	0.076	0.102
0/1	-	0.095	
<i>K. indica</i> vs. <i>P. hysterothorus</i>		<i>K. indica</i>	<i>P. hysterothorus</i>
	1/0	0.052	-
	0.83/0.17	0.057	0.082
	0.67/0.33	0.045	0.106
	0.5/0.5	0.047	0.131
	0.33/0.67	0.055	0.106
	0.17/0.83	0.057	0.102
0/1	-	0.102	

Table 2. Relative crowding coefficients of *C. album* (kc), *K. indica* (kk) and *P. hysterothorus* (kp) and their products.

Relative planting frequency	<i>C. album</i> vs <i>P. hysterothorus</i>			<i>K. indica</i> vs <i>P. hysterothorus</i>		
	Relative yields of <i>C. album</i> (kc)	Relative yields of <i>P. hysterothorus</i> (kp)	kc x kp	Relative yields of <i>K. indica</i> (kk)	Relative yields of <i>P. hysterothorus</i> (kp)	kk x kp
1/0	-	-	-	-	-	-
0.83/0.17	0.21 ± 0.01	2.46 ± 0.05	0.51 ± 0.02	0.59 ± 0.06	2.83 ± 0.25	1.64 ± 0.36
0.67/0.33	0.26 ± 0.01	1.61 ± 0.16	0.42 ± 0.04	0.84 ± 0.07	2.48 ± 0.30	2.07 ± 0.31
0.5/0.5	0.50 ± 0.02	2.32 ± 0.52	1.17 ± 0.31	0.58 ± 0.04	1.89 ± 0.24	1.10 ± 0.13
0.33/0.67	0.72 ± 0.03	2.66 ± 0.50	1.87 ± 0.28	0.94 ± 0.01	1.21 ± 0.02	1.14 ± 0.01
0.17/0.83	0.59 ± 0.24	2.06 ± 0.35	1.22 ± 0.21	0.49 ± 0.01	2.26 ± 0.51	1.09 ± 0.24
0/1	-	-	-	-	-	-

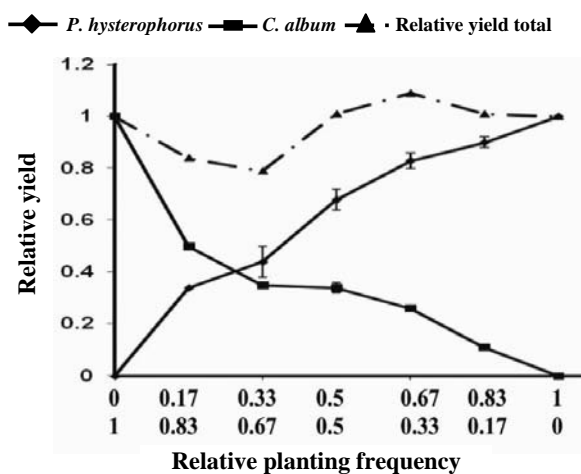


Fig. 5. Replacement diagram *Chenopodium album* vs. *Parthenium hysterothorus*.

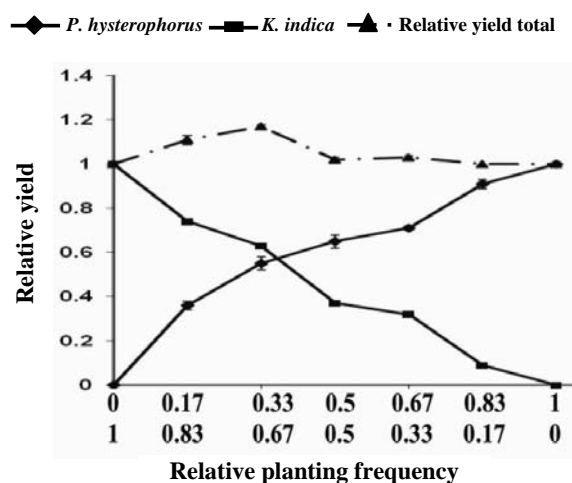


Fig. 6. Replacement diagram *Kochia indica* vs. *Parthenium hysterothorus*.

Intra-specific competition: The results of the density dependent experiment provide a comparison of the dry weights (Table 3) of the three species, whereby a statistically significant increase in the dry weight in each successive harvest was revealed. However, a non-significant decrease in the dry weight for *P. hysterothorus* was observed in the month of August. The trend could be due to early senescence in *P. hysterothorus*, where flowering and seed-shedding was much earlier as compared to *C. album* and *K. indica*.

In all harvests, the yields per plant at low densities were higher than those obtained at the corresponding high planting densities (Table 4). This indicated that at high planting densities, intra-specific competition increased and lowered the yield/plant. The difference between the yields/plant at high and low planting densities at the last harvest was greatest for *C. album* (2.81 and 5.66, respectively), showing low plasticity due to intraspecific competition, as compared to *P. hysterothorus* and *K. indica*.

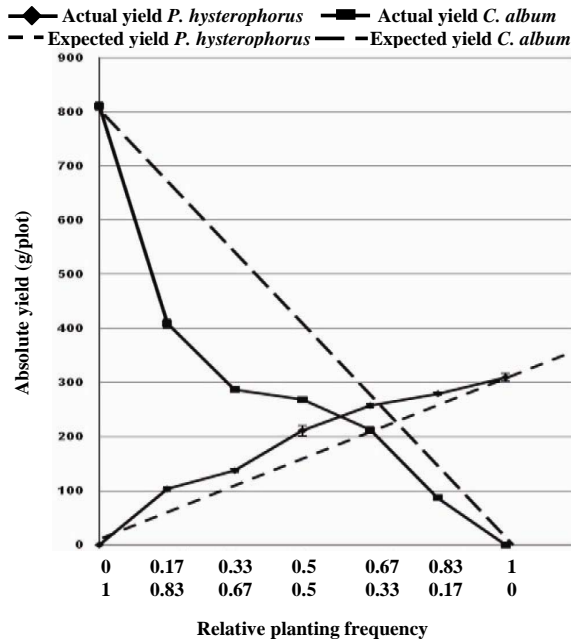


Fig. 7. Replacement diagram *Chemopodium album* vs. *Parthenium hysterophorus*.

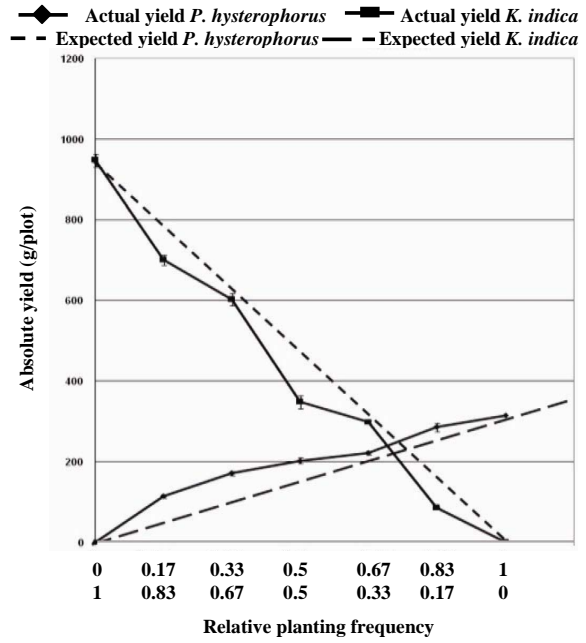


Fig. 8. Replacement diagram *Kochia indica* vs. *Parthenium hysterophorus*.

Table 3. Dry weights of whole plants of *P. hysterophorus*, *C. album* and *K. indica* in low and high planting density at monthly intervals.

Month of harvest	<i>P. hysterophorus</i>		<i>C. album</i>		<i>K. indica</i>	
	Low planting density	High planting density	Low planting density	High planting density	Low planting density	High planting density
April	5.97 ± 0.29	19.86 ± 1.18	3.50 ± 0.29	12.24 ± 0.97	3.62 ± 0.17	13.74 ± 0.81
May	63.18 ± 1.50	152.09 ± 2.33	15.50 ± 0.93	65.24 ± 1.76	30.50 ± 2.74	95.12 ± 2.23
June	139.08 ± 3.06	271.02 ± 2.19	30.61 ± 2.36	97.01 ± 3.84	74.77 ± 2.66	165.22 ± 3.66
July	286.32 ± 3.34	440.82 ± 4.94	60.37 ± 1.89	125.79 ± 3.26	114.32 ± 3.66	195.98 ± 1.59
August	276.32 ± 11.07	430.95 ± 6.37	113.29 ± 4.01	202.21 ± 3.52	184.66 ± 3.12	290.45 ± 5.19

Table 4. Yield/plant (on dry weight basis) of *P. hysterophorus*, *C. album* and *K. indica* in low and high planting density at monthly intervals.

Month of harvest	<i>P. hysterophorus</i>		<i>C. album</i>		<i>K. indica</i>	
	Low planting density	High planting density	Low planting density	High planting density	Low planting density	High planting density
April	0.30 ± 0.02	0.10 ± 1.10	0.17 ± 0.02	0.06 ± 0.01	0.17 ± 0.01	0.07 ± 0.003
May	3.15 ± 0.07	1.26 ± 0.02	0.70 ± 0.05	0.36 ± 0.01	1.52 ± 0.14	0.51 ± 0.01
June	6.03 ± 0.12	2.46 ± 0.09	1.53 ± 0.12	0.59 ± 0.03	3.74 ± 1.14	0.94 ± 0.02
July	14.56 ± 0.38	5.52 ± 0.15	3.01 ± 0.09	1.29 ± 0.05	5.71 ± 0.18	1.32 ± 0.01
August	14.03 ± 0.34	6.09 ± 0.23	5.66 ± 0.20	2.81 ± 0.05	9.23 ± 0.16	2.86 ± 0.11

For *P. hysterophorus* the trends in the values of β parameter, (Fig. 9) showed an increase for the months of May, June and July, the gradient being steepest in July, thus indicating fastest rate of growth and greatest occupation of space, followed by a slight decrease in β -Curve for *K. indica*, but of a lesser magnitude than *P. hysterophorus*. However, the β -Curve for *C. album* remained comparatively low and less steep thus indicating that *C. album* seemed to occupy least space.

The overall results of both Replacement Series and Space Occupation Experiments depict greater competitive abilities for *P. hysterophorus* as compared to *K. indica* and *C. album* thereby explaining its invasive success.

Discussion

Out of the eight species studied, *P. hysterophorus*, *K. indica* and *C. album* had highest rates of germination. During the experimental period, on average basis, *P.*

hysterophorus ranked higher as its germination rates remained consistent, whereas that of other co-existing species decreased at different times. Relatively higher rates of germination of *P. hysterophorus*, *K. indica* and *C. album* may be because their seed size is smaller as compared to the rest of the plant species studied (Vehra, 2002). These results are also in conformity with the findings of Thompson & Grime (1979), who reported that small-sized seeds from wind-pollinated plants have generally high rates of germination. This provides greater opportunity of establishment and germination throughout the year, thereby conferring higher competitive ability to *P. hysterophorus* as compared to the native species. The germination experiments carried out to test the effect of fruit pulp on germination, indicated that the presence of fruit pulp, assuming that it contains inhibitors which permit seeds to tide over winter (Ricardo & Veloso, 1987), decreased the germination rates of most of species to varying degrees whereas *P. hysterophorus* was among the least affected species. Absence of dormancy in *P. hysterophorus*, as also reported by Batish *et al.*, (2002) and lack of inhibitors (for its own germination) explains the readiness of germination and its regeneration throughout the year. On the basis of germination viability of seeds under all experimental conditions it is clearly indicated, that the co-existing annual species might not be able to compete successfully with *P. hysterophorus* as it has higher average germination percentage throughout the year and would interfere with the growth of other species once it invades an area.

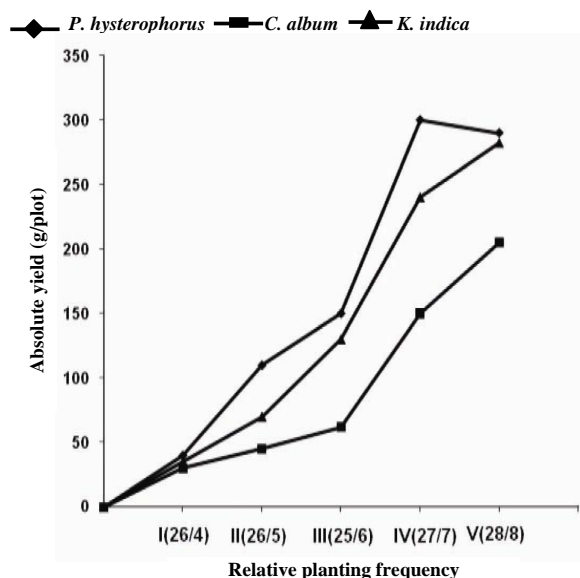


Fig. 9. β -Curves for *Parthenium hysterophorus* and *Kochia indica*.

The results of the present investigation showing highest root/shoot ratio, $RTY=1$, $k > 1$ and greater 'actual' yields than 'expected' yield in mixtures in replacement diagrams as well as steeper and higher β -Curve in *P. hysterophorus* as compared to *C. album*, *K. indica*, have provided sufficient information for assessing the long term impact of *P. hysterophorus* on the presently dominant species of wasteland.

Out of the two coexisting species, growth of *C. album* seemed to be suppressed to a much greater degree by *P. hysterophorus* as compared to *K. indica*, as revealed by the Replacement Series Experiment. Although the 'actual' yields for *C. album* and *K. indica* as shown by the Replacement Diagrams, were lower than that of the 'expected' yields, much lower values for *C. album* are indicative of its relatively greater suppression by *P. hysterophorus*, whereas *K. indica* seems to show, comparatively, more interspecific competition.

The final outcome of competition, being determined by the successive β -values at subsequent harvests shows that throughout the vegetative growth *P. hysterophorus* gains precedence over *K. indica* and *C. album*. It is only after flowering and seeding that the β -values for *P. hysterophorus* decline, but by that time *P. hysterophorus* takes the lead by producing seeds that germinate well ahead of the two co-existing species in the field.

Moreover, growth strategies, especially, seed size, indeterminate growth, expanded period of flowering and prolific seeding habit of *P. hysterophorus*, (Oudhia, 2001), along with constantly high rates of germination throughout the year assists it to compete with spring, summer and winter annuals as it is able to exploit the unused resources, arising in the form of bare areas created by either disappearance or senescence of co-existing annuals. In addition to the usual growth of seedlings, some plants of *P. hysterophorus* with perennating winter roots were also seen in the experimental plots after the harvest, where as the other two species senesce after setting seeds, and do not germinate till the next spring (Vehra, 2002). This kind of invisibility (Davis *et al.*, 2000) by *P. hysterophorus* can be explained on the basis of the susceptibility of the local species to invasion, as unused resources in the off season are being utilized by the invader species and moreover it encounters less intense competition during the season for these resources from the even the most dominant species in the habitat.

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