

Phenotypic plasticity and plant invasiveness: Case study of congress grass

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This paper highlights the phenotypic variation of congress grass (*Parthenium hysterophorus*) to varying soil texture. Plants demonstrated significant differences in some traits among the different soil types and these phenotypically plastic traits, in combination, contribute to invasiveness of the species, allowing for the range expansion observed in different habitats.

MANY organisms can respond with considerable flexibility to a changing environment, generating a range of characteristics depending on the environment in which the developing organism finds itself¹. A new species, when introduced into an alien environment, must become established within the constraints of physical site characteristics and competition with resident vegetation². The ability of an organism to express different phenotypes in response to environmental cues, i.e. phenotypic plasticity³, is generally interpreted as an adaptation for dealing with a variable environment. The primary benefit of being phenotypically plastic as an invading taxa lies in

the ability of plasticity for traits that contribute directly to fitness⁴ and broaden the niche width of the population, and therefore, its range of potentially available resources⁵.

The success of an alien species depends on the degree of invasiveness, i.e. the potentiality to establish and spread⁶. A few simple biological attributes can be strong predictors of potential invasiveness of a species^{6,7}. Plant height, relative growth rate (RGR) and seed mass, as indicators of both the establishment and regenerative phases of the life cycle⁸ are the most relevant traits that address competitive ability⁹⁻¹¹.

The nature of soil, associated with soil attributes such as texture, organic matter, pH and bulk density¹², is aptly known to be a potent determinant of plant adaptation and distribution¹³. Soil texture is a surrogate index of soil quality. It influences organic matter accumulation¹⁴, distribution of soil N (ref. 15) in association with topography and also independently¹⁶, and the dynamics of soil water¹⁷ that most frequently limits the biological processes in semi-arid regions¹⁸.

We hypothesize that the colonizing ability of an invader is a function of plasticity for fitness-related traits, enabling it to cope with and perhaps to benefit from habitat conditions. In order to test this hypothesis, we evaluated the response of a well-known invader species, *Parthenium hysterophorus* (congress grass; Asteraceae) in terms of plant height, RGR and seed mass, when cultured in soils differing in texture. *P. hysterophorus*, native of tropical America, is a rapidly colonizing weed and a health hazard¹⁹, especially in the tropics. In India, it was first recorded from Pune, Maharashtra²⁰. During the last 30 years, it has spread alarmingly to virtually every state in the Indian territory, occupying vast areas of waste- and cultivated lands.

A pot culture experiment in a completely randomized design, was established in the Botanical Garden, Banaras Hindu University (BHU), Varanasi (25°18'N, 83°03'E, 129 m asl), India. The proportions of clay and sand were varied by thoroughly mixing the S₁ soil (collected from subsoil layer, below 25 cm of a pond) and the S₅ soil, nearly pure sand (collected from a river bank) to create homogenous soil mixtures (in 3:1, S₂ and 1:3, S₃). An alluvial garden soil (Inceptisol) was the fifth soil type (S₄). Sand, silt and clay fractions in the soil mixtures were determined by the hydrometer method²¹ (Table 1). Thus five treatments reflecting a gradient of decreasing clay content (%), 14 (S₁), 10 (S₂), 3 (S₃), 2 (S₄), and 0 (S₅), were created.

For seed germination trial, fresh *P. hysterophorus* achenes (hereafter referred to as seeds) were collected from a single local population of plants of uniform height. The seeds were stored for six weeks in the dark at room temperature until the experiments commenced. On 25 May 2000, 45 seeds in each treatment (three replicates per treatment) were placed into earthen pots (2.87 l) filled with respective soil mixtures, moistened to field

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capacity. Per cent germination was calculated on the daily observations (till no more seed germinated). The length of seedlings was measured ten days after the germination.

On 21 June 2000, two-week-old seedlings (with a biomass equivalent to 40 mg dry wt per seedling), selected for uniformity, were transplanted (one per pot) into 15 earthen pots (11.22 l) per treatment containing the respective soil mixtures. The pots were irrigated every alternate day. To determine the influence of treatments on *P. hysterophorus*, three plants (per treatment) were destructively harvested at vegetative stage (29 days after transplantation) and three (per treatment) at mature stage (during flowering prior to achene dehiscence). At each harvest, after measuring the height, plant parts were separated and oven-dried at 80°C to constant weight. RGR (mg g⁻¹ day⁻¹) was calculated as follows²²:

$$\text{RGR} = \frac{\ln(W_2) - \ln(W_1)}{T_2 - T_1},$$

where W_1 is the dry weight of two-week-old (i.e. T_1) seedlings and W_2 is the dry weight at 29 days after transplantation in the case of juveniles, and that at the flowering stage prior to achene dehiscence in the case of post juveniles (i.e. T_2), and $T_2 - T_1$ is the sampling interval in days.

Reproductive growth was studied by measuring seed production (mean number of seeds per capitulum \times the number of capitula per plant) and mean seed dry mass (80°C), in each of the remaining nine individuals (out of 15) per treatment (except S_1 , where data were based on merely three plants which survived till seed production). Reproductive effort (RE) was estimated as the ratio of number of seeds per gram above-ground dry weight²³.

Effect of treatment on growth variables was analysed by one-way ANOVA. Differences between treatment means were tested by Tukey's HSD test (at $P < 0.05$). Linear regression was used wherever necessary. All statistical analyses were conducted using the SPSS statistical package (SPSS Inc., Chicago, USA).

Table 1. Textural properties of soil mixtures

Treatment	Proportion (%)		
	Clay	Silt	Sand
S_1	14a	62a	24a
S_2	10b	62a	28a
S_3	3c	21b	76b
S_4	2c	73c	25a
S_5	0d	1d	99c

Values in a column with different letters are significantly different from each other according to Tukey's HSD test at $P < 0.05$.

Seed germination ($F_{4,10} = 90.22$; $P < 0.001$) and seedling length ($F_{4,10} = 7.04$; $P = 0.006$) were significantly affected by the clay content. Germination was greatest (62%) in S_4 (i.e. 2% clay) and was significantly reduced in soils above and below this clay content (Figure 1a). The lowest germination (9%) occurred in S_1 . However, germination was 64 and 39% lower, respectively in S_2 and S_5 , compared to S_4 treatment. Further, differences in seedling length were not significant among treatments except for S_5 , where it was only half as that in S_4 (Figure 1b).

P. hysterophorus exhibited substantial phenotypic variability in plant traits in response to soil quality (see ref.

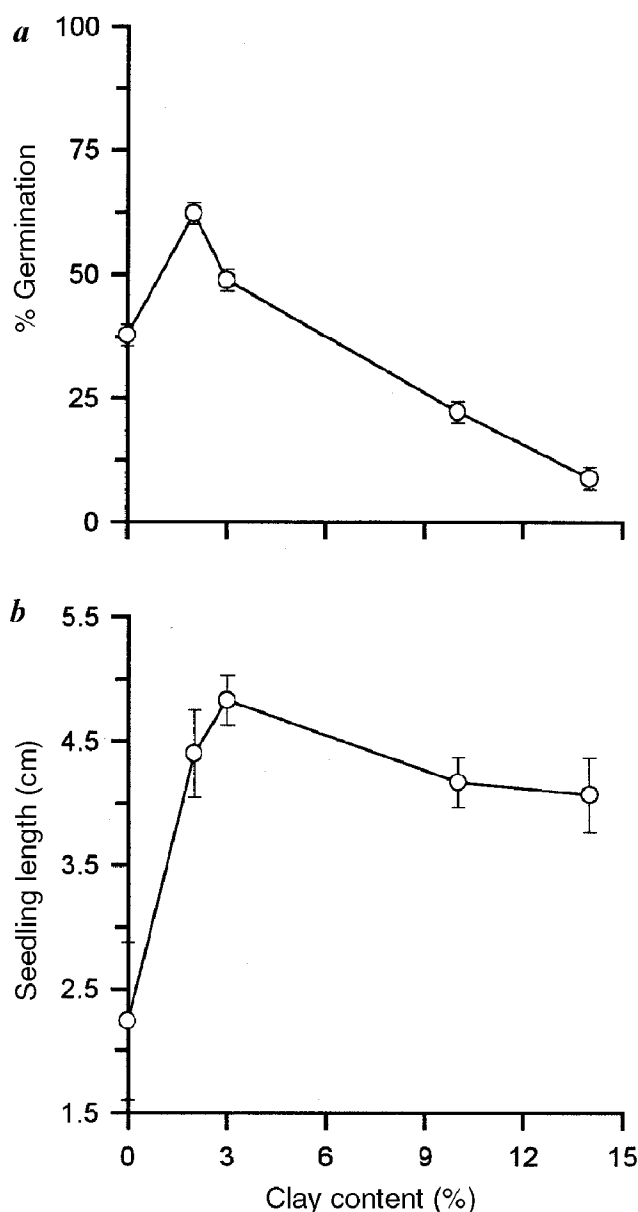


Figure 1. Effect of clay content on per cent seed germination (a) and seedling length after 10 days (b) of *P. hysterophorus*.

24 for additional data). Trends in plant height and RGR were similar at vegetative and reproductive stages (Figure 2a and b), where the peak was attained in S_3 treatment. Increased clay content (i.e. >3%) led to consistent decline in these estimates. ANOVA indicated that plant height differed between the vegetative and reproductive stages ($F_{1,20} = 12174.33$; $P < 0.001$) and among treatments ($F_{4,20} = 324.06$; $P < 0.001$). RGR also differed between the vegetative and post-vegetative stages ($F_{1,20} = 15048.73$; $P < 0.001$) and was significantly affected by treatment ($F_{4,20} = 1150.01$; $P < 0.001$). The stage \times treatment interaction was highly significant, indicating differential responses of the variables. Juveniles were 52 and 39% shorter, respectively in S_1 and S_5 than those in S_3 .

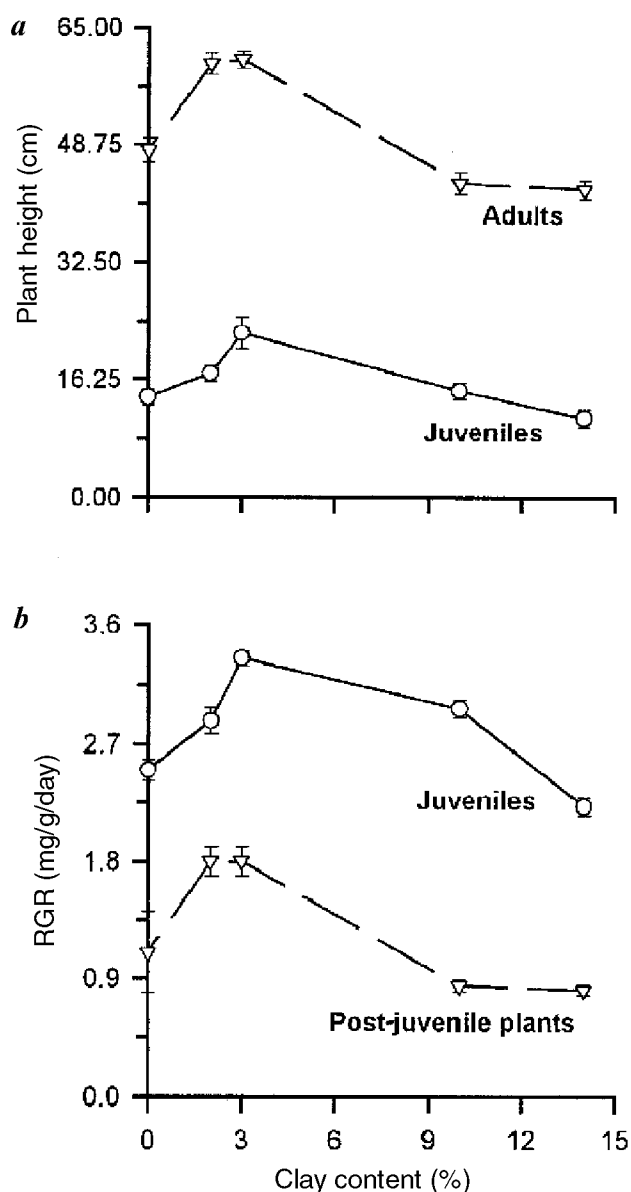


Figure 2. Effect of clay content on plant height (a) and relative growth rate (RGR) (b) of *P. hysterophorus*.

Similarly, RGR during the vegetative stage was 35 and 27% lower in S_1 and S_5 treatments respectively, compared to S_3 . Plant height at mature stage in S_1 and S_5 was respectively 30 and 20% lower than in S_3 . Correspondingly, post-juvenile plants of S_1 and S_5 had 56 and 39% lower RGR respectively, compared to those grown on S_3 .

HSD analyses showed that the above-mentioned traits differed significantly among treatments, except that plant height in juveniles did not vary among S_2 , S_4 and S_5 , and in adults between S_1 and S_2 , and S_3 and S_4 . RGR did not differ significantly between S_2 and S_4 treatments in juveniles and that between S_3 and S_4 in post-juvenile plants. However, RGR was 14% lower ($P < 0.05$) in S_4 compared to S_3 during the vegetative stage. Invariably higher RGR in juveniles than mature plants suggested that greater pace of growth during early phases of the life cycle would confer an advantage to the establishing plant.

There were significant treatment effects on plant traits for RE ($F_{4,10} = 16.71$; $P < 0.001$) and seed mass ($F_{4,10} = 19.03$; $P < 0.001$). RE increased up to S_4 and then declined significantly as clay content increased (Figure 3a). In contrast, with increasing clay content, seed mass continuously increased (Figure 3b). These traits were 50% lower in S_5 compared to S_4 .

According to Bazzaz²⁵, availability of soil resources, especially nutrients, critically influenced plant growth, population dynamics and competitive interactions. We expect that the amount of plant-available N could be low in soils high in clay content where restricted aeration²⁶ may increase denitrification losses²⁷ and reduce mineralization of organic N (ref. 28). Siemens *et al.*²⁹ reported that limited resources (e.g. soil nutrients, water) can directly inhibit the rate of growth. Hence, low RGR exhibited on clay-rich soils (S_1 and S_2 treatments) suggests that *P. hysterophorus* would maintain slower growth rates under nutrient-poor habitats as a survival strategy. Further, inadequate contact of roots with the soil in sands³⁰ could limit the uptake of water and nutrients, which in turn, appears to reduce the seedling length and growth rates in *P. hysterophorus*.

On the other hand, high RGR observed in S_3 and S_4 treatments would enable the plant to pre-empt growth resources. The fact that height is an indicator of relative size may explain the greater ability of larger plants to extract resources³¹ from these soils. Consequently, *P. hysterophorus* can take advantage of resource abundance and grow more rapidly than its neighbouring plants. This trade-off is thought to be a necessary condition for the persistence of parthenium weed across fertility gradients.

Our observation that RE decreased with high clay content (>3%) agrees with the prediction that in environments where juvenile mortality is high, RE should be low³². In the S_1 treatment (with 14% clay), two-thirds of transplanted plants died during the vegetative stage (data not shown). Further, juveniles established successfully with comparatively higher RE on coarser soils. Plasticity

in terms of texture-induced variability in RE may suggest that *P. hysterothorus* could colonize under conditions of both high density-independent mortality (e.g. in open, disturbed habitats) and density-dependent regulation (e.g. in closed, less disturbed communities). The plant height in adults was positively related to RE ($r^2 = 0.70$; $P < 0.001$) indicating the influence of plant size on seed production and proportion of energy allocated to seeds. Thus, large plants seem to be at a reproductive advantage³³.

Light seeds are more dispersible³⁴ compared to heavier seeds³⁵ and production of numerous light seeds in *P. hysterothorus* grown on coarse-textured soils may thus facilitate colonization of new sites. On the other hand, the less dispersible heavier seeds produced in clay-enriched

Table 2. Selected habitat factors and performance of *P. hysterothorus* in two field microsites

	Shade and moist	Open and moist
Clay content (%)	1.4a	2.1b
Sand content (%)	58.0a	53.0b
Soil C (mg g ⁻¹)	10.6a	6.7b
Soil N (mg g ⁻¹)	0.7a	0.6b
Plant height (cm)	119.5a	96.0b
Number of seeds (plant ⁻¹)	29367.0a	19254.0b
Seed mass (mg seed ⁻¹)	0.31a	0.5b
Density (plant m ⁻²)	970.3a	866.3b

Values in a row with different letters are significantly different from each other according to 't' test at $P < 0.05$.

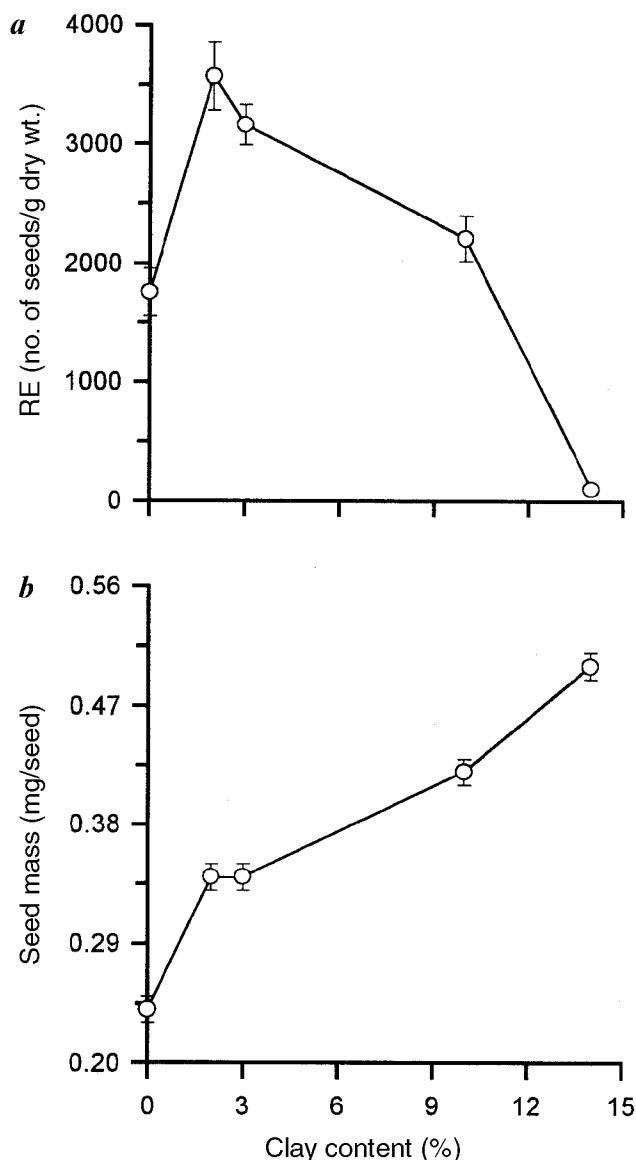


Figure 3. Effect of clay content on reproductive effort (RE) (a) and seed mass (b) of *P. hysterothorus*.

soil will likely form a persistent seed bank as argued by Navie *et al.*³⁶. We found that soils high in clay content reduced the germination of *P. hysterothorus* seeds, probably because of restricted aeration²⁶. The production of larger seeds (with greater reserves), although fewer in number, in clay-rich soils would confer an added benefit to this invasive species. In frequently disturbed areas where chances of seed burial are more³⁶, larger seeds may ensure the long-term persistence of *P. hysterothorus* through emergence from greater depths of burial³⁷. These observations support that the availability of seed reserves can have important impact on seedling establishment¹¹ and thus, persistence or invasiveness of a species.

This study has revealed that plasticity in plant traits due to soil quality led to two contrasting strategies which make *P. hysterothorus* a successful invader. The first resulted in tall, fast-growing competitors with small seed mass, appropriate for a rapid population expansion. The second strategy yielded short plants with high seed mass for persistence in an otherwise less favourable habitat leading to a slow build-up of population, with a gradual increase in the size of the seed bank.

P. hysterothorus has been reported from a wide variety of habitats¹⁹. Because of the inherent plasticity, this weed can rely on phenotypically varying plant traits to exploit the available 'invasion windows' (conditions suitable for establishment, growth, and proliferation of invaders, see ref. 38). We believe that the ubiquity of heterogeneity in natural habitats³⁹ might create a mosaic of microsites, with populations of relatively taller plants growing in the more favourable spots and those of smaller plants in less favourable ones. This is illustrated in Table 2 from two habitat microsites located within the BHU campus. Management practices should focus on limiting seed dispersal from taller populations and preventing the build-up of persistent seed bank in shorter populations in clay-rich soils.

We may point out however, that in addition to variable soil conditions, the presence of other species in natural habitats may also elicit a plastic response by influencing

the growth performance of *P. hystrophorus* through competitive and other indirect effects.

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