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Differential biomass allocation to plant organs and their allelopathic impact on the growth of crop plants: A case study on the invasibility of *Ageratum conyzoides* in Indian dry tropics

NIDHI CHAUDHARY[1], RUP NARAYAN[2] and D K SHARMA[3]

I P (PG) College, Bulandshahr, Uttar Pradesh 203 001

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ABSTRACT

Variation in biomass allocation strategy of the alien winter annual billy goat weed (*Ageratum conyzoides* L.) was investigated for its invasiveness at two contrasting sites of occurrence in Indian dry tropical peri-urban region at long-term and recurrently infested site (LTI) and short-term infested (STI) site. Growth retardation impact of leaf, stem, root and reproductive part of this weed on maize and mung growths was also investigated. Compared to LTI site, the plants at STI site had higher mean basal diameter, leaf number, total plant biomass, leaf and reproductive mass fractions. Phenotypic plasticity was also higher here, albeit marginally. On the other hand, LTI plants had higher mean shoot length, belowground: aboveground biomass ratio, stem and root mass fractions. Biomass allocation to different components varied with ontogeny and site/soil conditions. While stem allocation increased with plant size at both sites, the leaf allocation generally declined. At any ontogenetic point, the reproductive and leaf allocations by plants were higher at STI compared to LTI. Root allocation at STI increased with plant size, whereas it decreased at LTI. Soil organic carbon significantly improved with increasing amount of residue of leaf, stem, root and reproductive part incorporated in soil. The leaf and root residue-amended soils recorded increasing growth retardation with increase in the amount of their incorporation in the soil.

Key words: Allelopathic impact, Biomass-allocation, Dry tropics, Exotic invasive, Phenotypic plasticity

Billy goat weed (*Ageratum conyzoides* L.) (*Asteraceae;* hereafter *Ageratum*) is presently considered as one of the most problematic weeds in India (Kohli *et al*. 2006). It is widely spread the world over, especially in the tropical and sub-tropical regions, is a polymorphic, aromatic annual herb, native to tropical America, naturalized as a natural weed throughout India up to an altitude of 1800 m (Anonymous 1948). Although it is primarily an annual weed of cultivated fields, it has survived well in a range of habitats, that include rangelands, pastures, and along water courses (Kohli *et al*. 2006). *Ageratum* is presently considered as an established exotic invasive weed species in India (Khuroo *et al*. 2012). Primarily considered as a shade-loving seasonal plant dominantly occurring in regions of low temperature, its predominant territorial expansion has, however, begun to be witnessed in Indian dry tropics also, particularly in the anthropogenic regions (Satyanathan *et al*. 2013). In the peri-urban region around Delhi in Northern and sub-tropical India, it has invaded into open areas in human habitations, fruit-orchards, banks of river, canal, and in and around various agro-ecosystems. The plasticity of an ecologically important trait of *Ageratum* such as biomass allocation strategy is likely to facilitate the evolution of greater plasticity enabling higher invasibility (Droste *et al*. 2010). This characteristic may allow it to occupy a multiplicity of new environments (Funk 2008, Pyšek and Richardson 2007, Rejmanek *et al*. 2005), as very intimate relationship is suggested to exist between the phenotypic changes and resource acquisition. Such changes facilitate stress tolerance and invasiveness of a species (Chaudhary 2014, Tyler *et al*. 2007). Despite recognizing this plant species as one of the most rapidly advancing exotic invasive weeds in India, interfering with local biodiversity and crop growth (Batish *et al*. 2009), the ecological studies pertaining to investigation of its enhancing invasibility via its differential biomass allocation to different plant organs and across contrasting soil-resource regimes or habitat conditions, has been completely lacking.

The chemical profiles of its plant components, e.g. leaf, stem, root and flower has been reported by Amadi *et al*. (2012). However, investigations pertaining to the relative impact of these plant components separately have not been adequately investigated, although they join the dead organic pool in nature that undergoes decomposition after plant death and decay. Batish *et al*. (2009) observed the inhibitory impact of leaf residues on the growth of *Oryza sativa*.

[1]e mail: nidhi.c06@gmail.com, Department of Botany; [3]e mail: dsharma@iari.res.in, Centre for Environment Science and Climate Resilient Agriculture, IARI, New Delhi 110 012

We hypothesize that high phenotypic plasticity coupled with its growth influence on the plant/crop associates through modification of soil properties on entry into the soil system after the death and decay of *Ageratum* account for the aggressive invasibility of this exotic weed in low-nutrient anthropic ecosystems in Indian dry tropics.

The major objectives of the present study were: (i) to study the variations in plant traits of *Ageratum* populations at a site that witnessed recurrent infestations for long time and those at short-infested site of naturalization in an anthropogenic dry tropical peri-urban region, and (ii) to investigate the relative impact of residues of different plant components (leaf, stem, root and reproductive part) of *Ageratum conyzoides* on: (a) soil, and (b) the growth of *Zea mays* (maize) and *Vigna radiata* (mung).

MATERIALS AND METHODS

The study area was located at Bulandshahr (28°04' and 28°43' N lat. and 77°08' and 78°28' E long.), western part of Uttar Pradesh which falls within Ganga basin, India. It is at a distance of 72 km from the national capital, Delhi. This region has about 300 brick industries, more than a dozen milk dairies and a range of small-medium scale industries at Sikandrabad, and pottery and ceramic industries of international repute at Khurja. The region has witnessed rapid upsurge in transportations due to developmental activities in the last 4-5 decades. The vegetation, here, is mainly comprised of annual weeds and ruderals (Gupta and Narayan 2011). Two *Ageratum*-infested study sites, representing contrasting habitat conditions, were selected for the present study. The first site, designated as long-term infested site (LTI), was located near Gang Nahar canal along Khurja road. It experienced over ten years of long recurrent *Ageratum* infestations. The vegetation, here, was relatively species-rich and faced low disturbance by humans and grazing animals. This site soil had higher mean moisture content (2.37 %), pH (7.05), org. C (1.28 %), tot. N (0.06 %), exch. K (133.37 kg/ha), and avail. P (8.87 kg/ha), S (11.6 ppm), Zn (0.74 ppm), Fe (4.97 ppm), Mg (4.81 ppm), Cu (0.64 ppm). The second site, designated as short-term infested site (STI) was located in the midst of long fallow land, which had recently begun to witness human colonization activities. Fruit orchard and a railway track lay in the vicinity of this study site. Relatively more disturbed STI site-soil had mean moisture content (1.65 %), pH (7.39), org. C (0.36 %), tot. N (0.04 %), exch. K (130.62 kg/ha), and avail. P (8.5 kg/ha), S (11.31 ppm), Zn (0.74 ppm), Fe (4.65 ppm), Mg (4.73 ppm), Cu (0.64 ppm). The maximum and minimum mean temperatures during the growth period of *Ageratum* (September to April) in our study were 28.8ºC and 14.4º C respectively. The climate of the region and the study area was semi-arid.

Eight samples of surface-soils (0-10 cm) were randomly collected from each site in the months of February, May and October. The soil samples were air-dried and sieved in a 2 mm sieve. Physico-chemical properties of soils estimated in this study included: soil moisture content, pH, total organic carbon (Walkley and Black method), total N (micro-Kjeldahl's method) according to Piper (1944); available phosphorous and exchangeable potassium according to Allen *et al*. (1986). Various micro-nutrients like available sulphur, zinc, iron, magnesium and copper were estimated at the District soil testing lab in Bulandshahr, according to Piper (1944).

A total of two hundred individuals of *Ageratum* were selected at different points of their growth, 100 from each study site (LTI and STI). The selected individuals were carefully dug with the help of a sharp, long (20 cm) iron spade (base width 8 cm) out of the ground with utmost care to minimize the loss of roots. This was accomplished by digging below to the root-system (shallow-fibrous roots) in a cylindrical manner approximately equal to the diameter of the top growth around the base of the plant to retrieve the smaller roots so as to make the root-loss minimum (Mahoney and Kegode 2004). They were then washed off gently and carefully with water to remove soil particles. Number of nodes and number of leaves (egg-shaped and ovate) of each plant individual were recorded. Shoot length (SL) of the fresh individuals was measured from the top of the plant to the point of discoloration, indicating the soil surface. In the similar way, root length (RL) was measured from the top of the root-system to the point of discoloration. Basal diameter of the plant individuals was also measured. Plants were separated into different components like roots, stems, leaves (petiole and lamina) and reproductive parts. The reproductive parts included peduncle, buds, flowers (purple, less than 6 mm across, with around 40 to 70 flowers arranged in close terminal flower-heads) and the fruits (small coffee-brown, one-seeded achenes). The four plant components were then oven-dried at 70ºC for 48 hr and weighed to determine component biomass, aboveground (AGB), belowground (BGB) and total biomass (TB). The component mass fractions of leaf (LMF); stem (SMF), reproductive part (RPMF) and root (RMF) were estimated as the biomass of each component relative to the total biomass. Leaf area ratio (LAR) of a plant was calculated as the area of leaves per unit dry weight of the whole plant. Leaf mass per area (LMA) was calculated for each site as the dry weight of leaves per unit area of fresh leaves.

Fresh leaves (100) were randomly collected from each site. They were scanned with a digital leaf area meter (Systronics) to determine leaf area, dried at 70º C for 48 hr and weighed to determine the leaf mass per area (LMA).

The plant component fractions (LMF, SMF, RPMF and RMF) were studied in relation to variation in shoot length. The component mass fractions were regressed against shoot length using second order polynomial regression model to determine the biomass allocation alterations with increase in plant size.

To compare the degree of plasticity among mature individuals (in reproductive phase) at two sites, a plasticity index (PI_V) was generated for each trait (Valladares *et al*. 2006). The index ranges from zero (no plasticity) to one (maximum plasticity). It is evaluated as the difference between the maximum and minimum values of the trait divided by the maximum value at the site. The mean plasticity indices for plant-and leaf-level traits were evaluated for each site by averaging all variables. Pearson product–moment correlation coefficients were generated to evaluate the linear association between traits and total biomass of a plant individual across the study sites.

Fresh mature plants (reproductive phase) of *Ageratum* were randomly collected from the two weed-infested sites (LTI and STI), on 16 March 2010. Leaves, stems, reproductive parts and roots were separated from the plants. They were oven-dried at 70°C for 48 hr, powdered and stored in polythene bags at room temperature for use in soil experiments.

The powdered biomass components of *Ageratum*: Leaf (L), Stem (S), Reproductive part (RP) and Root (R) were added at 1, 3, 5 g per kg soil on March 20, 2010. One kg soil was put in each polythene bag (perforated bottom) for pot culture investigations. The experimental soil was collected from the crop field (pH 7.39, org. C 0.68 %, tot. N 0.02 %, exch. K 131 kg/ha and avail. P 9.33 kg/ha, S 10.96 ppm, Zn 0.75 ppm, Fe 4.62 ppm, Mg 4.73 ppm, Cu 0.64 ppm). The untreated soil was considered as control (US). Three replicates for each soil amendment and control were prepared. These polythene bag-soils were watered to field capacity throughout the experiment and unwanted, emerged plants were eliminated periodically.

The treatment consisted of 3 factors: (i) Donor weed (*Ageratum*), (ii) Applied doses 3 (1, 3, 5 g/kg soil) and (iii) Recipient crops 2 (*Vigna radiata* L.) var. SML 668 and (*Zea mays* L.) var. Victory Super. Fifteen days after watering and weeding (4 April, 2010), four seeds of mung and maize were sown separately in the amended soils in triplicate. Percent germination was recorded until no further seeds germinated. Germination speed was calculated according to the formula: Germination speed = Germination percent/ Day of completion of germination (ISTA 1976). For growth studies, only one healthy individual was allowed to grow and the rest of the germinated plants were eliminated. The shoot length was measured 30 days after sowing (DAS). The experiments were carried out under shaded-house conditions with natural light supply. During the period of crop growth study, the mean maximum and minimum temperatures recorded were 33.49° C and 17.37°C, respectively.

One month after soil amendments on 22 April 2010, soil samples were collected, air-dried and analyzed for soil organic C using the rapid titration method (Walkley and Black). Statistical and graphical analyses for above studies were carried out using MS Excel, SIGMAPLOT 11 and SPSS 20.

RESULTS AND DISCUSSION

"Biomass allocation" basically refers to the realized distribution of biomass over the various organs of plant. In the present study, its differential allocation to leaves, stems, roots, and reproductive parts, and their ontogenetic trajectories revealed how *Ageratum* populations interacted with the prevailing climate, soil and site conditions for their growth optimization (Poorter and Sack 2012). Further, the differing growth retardatory impact of the plant components (that enter the soil system after plant death) on the two crops (mentioned above), presumably by altering the soil characteristics, is suggested to account for the accelerated invasive ability and adaptability of the investigated alien species invading to the newer areas in Indian dry tropics.

Species traits

Amongst plant-level traits, on the mean basis, shoot length of plant individuals of *Ageratum* at LTI site was significantly higher ($P < 0.01$) compared to that at STI site (Table 1). In contrast, the plant individuals at STI site recorded higher basal diameter and increased number of leaves. The root length and the number of nodes were, however, comparable at both sites. Greater height may also be considered to have rendered it an advantageous invasive characteristic for establishment in the invaded ecosystems after naturalization (Pyšek and Richardson 2007). Amongst

Table 1 Plant–level traits of *Ageratum conyzoides* (Mean ± SE) at long-term infested (LTI) and short-term infested (STI) sites in a dry tropical peri-urban region

Traits	LTI	STI	*P* value (*t* test)
Plant- and leaf-level traits			
No. of leaves	314.70±40.25	731.04±47.28	< 0.01
No. of nodes	12.12±0.55	11.92±0.39	ns
Shoot length (SL) (cm)	57.36±3.50	33.24±2.34	< 0.01
Root length (RL) (cm)	12.13±0.38	12.73±0.94	ns
Basal diameter (cm)	0.43±0.02	0.63±0.02	< 0.01
Leaf biomass (g)	2.29±0.31	7.67±0.61	< 0.01
Stem biomass (g)	4.79±0.54	3.95±0.62	ns
Reproductive parts biomass (g)	1.58±0.39	6.41±0.67	< 0.01
Root/belowground biomass (g)	0.93±0.10	1.72±0.25	< 0.01
Total biomass (g)	9.59±1.06	19.74±1.90	< 0.01
RL/SL ratio	0.33±0.03	0.43±0.03	< 0.05
BGB/AGB ratio	0.16±0.01	0.07±0.01	< 0.01
Leaf mass fraction (LMF)	0.24±0.02	0.58±0.02	< 0.01
Stem mass fraction (SMF)	0.56±0.02	0.12±0.01	< 0.01
Root mass fraction (RMF)	0.14±0.01	0.06±0.01	< 0.01
Reproductive parts mass fraction (RPMF)	0.07±0.01	0.25±0.02	< 0.01
Leaf area ratio (LAR) (m^2 leaf/kg plant)	17.13±0.74	62.31±4.77	< 0.01
Leaf area (cm^2)	9.63±0.27	7.90±0.18	< 0.01
Leaf mass per area (LMA) (g leaf m^{-2} leaf)	31.63±1.06	25.48±1.67	< 0.01

the biomass of the plant components, the *Ageratum* population at STI site had much higher total biomass, mainly on account of higher biomass of leaf, root and reproductive parts. The RL/SL ratio at this site was also significantly higher than that at LTI site, however, BGB/AGB ratio showed the reverse trend. In terms of mass fractions of different plant components, LMF and RPMF of *Ageratum* were higher at STI site, whereas the SMF and RMF at LTI site were higher. Amongst the leaf-level traits, leaf area and LMA at LTI site were significantly higher compared to that at STI site, although LAR was higher at STI site.

All plant-and leaf-level traits of plant individuals of *Ageratum* evaluated for both sites (LTI and STI) were significantly correlated with TB ($P < 0.05$) except RL/SL ratios that showed insignificant and negative correlation. The plant-level traits in general, including the biomass of plant components, showed strong and positive correlations with TB. However, the plant component mass fractions showed varying relations. BGB/AGB ratio, SMF and RMF showed negative correlation with TB at LTI site (correlation coefficients, r = -0.533, -0.257 and -0.547 respectively), whereas, its correlations were positive at STI site (r = 0.547, 0.736 and 0.556 respectively). On the other hand, LMF was negatively correlated at STI site (r = -0.743) but showed insignificant relation at LTI.

Plasticity indices

The plasticity index (PI_V) calculated for *Ageratum* population at both sites (LTI and STI) ranged between 0.35 and 0.99 for plant-level traits. The plasticity indices of different traits were generally higher at STI site, which included RL/SL ratio (0.96), higher than that reported for *Chenopodium murale* in Indian dry tropics (0.24-0.27) (Gupta and Narayan 2012). It was indicative of greater tendency of the relatively longer roots of the studied invasive weed to travel farther to acquire the scantily available nutrients nearby to attain the optimal performance of nutrient absorption in relatively sterile dry soils here. BGB/AGB ratio (0.99), SMF (0.99), RMF (0.99), LAR (0.74) and LMA (0.57). However, plant individuals at LTI site showed higher plasticity in terms of LMF (0.98) and RPMF (0.99). The overall mean phenotypic plasticity index (PI_V) was marginally higher for plant population at STI site (0.87) compared to that at LTI site (0.81). The ecological interpretation of these ratios has often been considered complicated. The use of mass fractions, on the other hand, is often suggested to avoid some of the complications related to ratios, as the fractions are not confined to only two i.e. aboveground and belowground aspects of the plant (Poorter and Nagel 2000).

Biomass allocation pattern

Different biomass fractions were considered to highlight alteration in allocation over time and how they vary with the given conditions. There was much variation in the biomass allocation pattern of different plant components of *Ageratum* with plant size and site of occurrence (Fig 1). In the present study, the LMF recorded at STI (0.58) was relatively towards the higher end of the LMF range 0.43-0.64, reported by Poorter and Remkes (1990) for 24 non-woody and perennial herbaceous species. Poorter and Nagel (2000) reported the LMF of 0.46 for herbaceous plants (n=500). However, the LMF recorded at LTI (0.24) was comparable to *Chenopodium murale* at nutrient-rich and -poor sites (0.28-0.35) in Indian dry-tropics (Gupta and Narayan 2012). The LMF slightly decreased over plant size for the plants at LTI site that had relatively high soil organic carbon, whereas the decrease was much sharper for plants at STI site with lower soil organic carbon (Fig 1a).

The SMF of *Ageratum* populations, at both the sites increased with increase in plant size. However, it was higher at LTI site compared to that at STI site at every stage of its growth (Fig 1b). The increasing investment of biomass to stem with ontogeny at both the study sites reflected the importance of support structure for this exotic weed, implicitly indicating its perennial tendency. The RPMF showed variable trend with increasing plant size, at STI site, it increased to a shoot length around 70 cm, and then decreased with plant size. In contrast, at LTI site, the initial RPMF that was lower compared to that at STI at the early stages of growth, increased sharply with the maturity of the plant. The RPMF and LMF at STI site were generally higher than those at LTI site at any ontogenetic point of consideration, particularly for plant individuals with shoot length ≤ 80 cm. The RMF of plants at STI and LTI sites showed a contrasting trend. While it decreased with age at LTI site, it increased at STI site. The mean RMF of *Ageratum* at both the sites was lower than the range 0.16-0.38 reported by Poorter and Remkes (1990), thus, indicating an overall lower root allocation by the investigated weed in comparison to non-woody perennial herbs. The allometric analyses in this study revealed shift in allocation of biomass to different plant components as the plants grew and matured. Such a variation in biomass allocation strategy of a plant species is often suggested to facilitate the evolution of greater plasticity and invasiveness (Droste *et al*. 2010), as it allows it to occupy a wide range of environments (Funk 2008, Rejmanek *et al*. 2005). This indicated highly dynamic nature of allocation shifts, to cope up with the alien environment at newly intruded sites. Such a plastic response of plants to environmental changes in areas with differing ecological conditions, like the presently investigated one in and around urbanizing landscape which is being continuously invaded by alien species, can be considered as the most potential mechanism for successful colonization and establishment (Lehmann and Rebele 2005, Maron *et al*. 2004).

Impact of plant component residues on mung and maize crop plants

The aggressive invasive ability of *Ageratum* appears to be further strengthened by its allelopathic potential to restrict and retard the growth of its plant associates. Variable impacts by different plant components (leaf, stem, root and reproductive part) that enter the soil system after the death

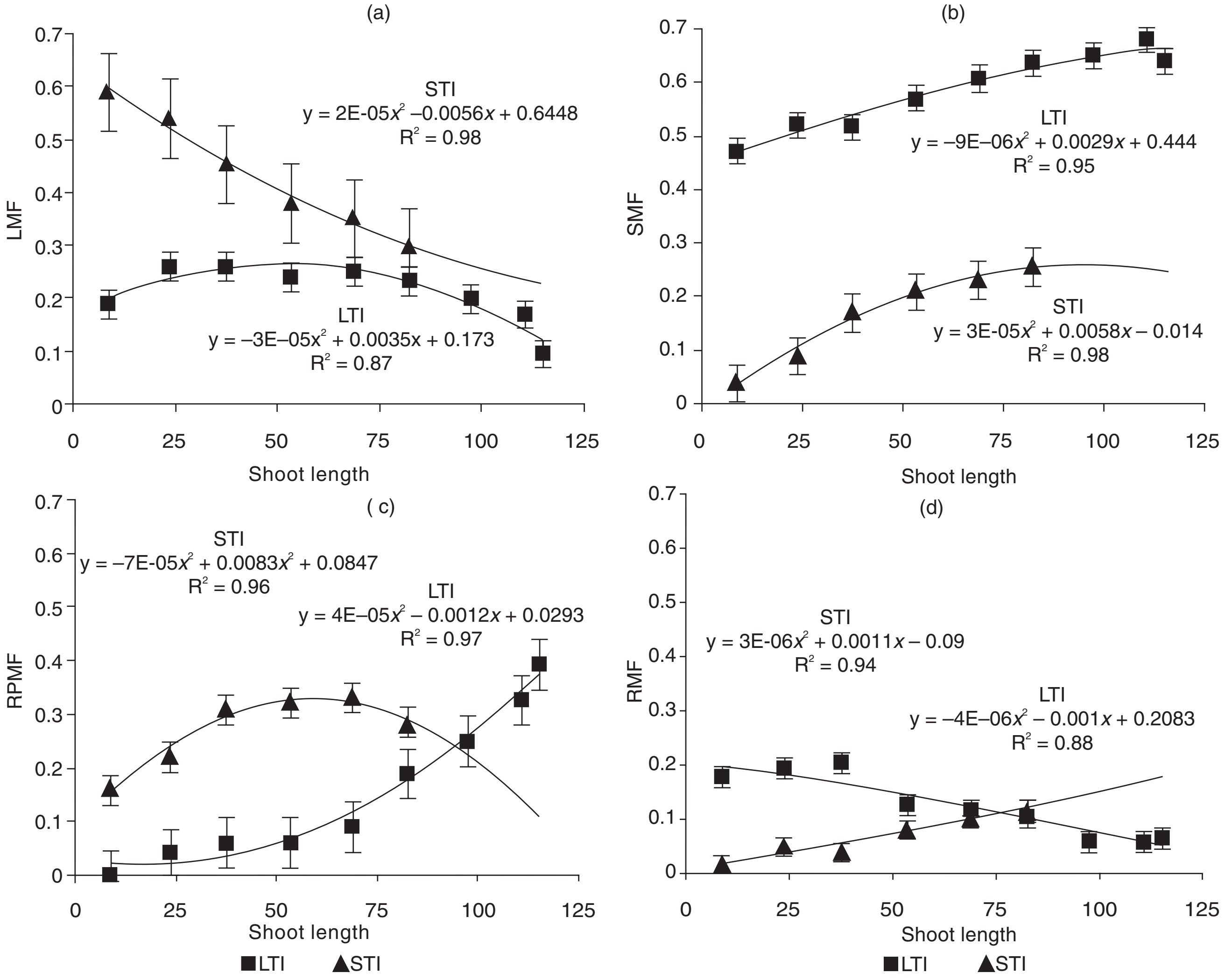

Fig 1 Variation of a) leaf mass fraction (LMF), b) stem mass fraction (SMF), c) reproductive part mass fraction (RPMF) and d) root mass fraction (RMF), in relation to shoot length of *Ageratum conyzoides* at long-term infested (LTI) and short-term infested (STI) sites in a dry tropical peri-urban region. Curves represent best-fit second-order polynomial regression

of *Ageratum conyzoides* were recorded in this study.

Seed germination and shoot length

The impact of the residues of plant components of *Ageratum* on seed germination and seedling growth varied with the crop, plant component and their doses (Table 2). The germination of seeds of maize was relatively more impacted compared to that of the mung seeds, and the inhibitory impact increased with increasing amount of doses of shoot, root and reproductive part residues. Leaf residues did not impact germination of maize seeds. On the other hand, mung seed germination appeared to be highly affected by the residues of leaf, root and reproductive parts. Stem residues did not influence germination of mung seeds. The maximum impact (50 % inhibition) of plant component residue was observed for root residue at 5g/kg for both maize and mung seeds. A similar impact of plant component residues was recorded on germination speed of these two crop seeds.

The shoot lengths of mung and maize plants also showed variable growth trends in soils amended with varying quality of residues (plant-component type) and their doses. The shoot length of both the crops decreased with increasing dose of the residue plant component of *Ageratum*. This growth inhibitory impact in both the crops was higher for leaf and root residues. The leaf and root components may be considered relatively soft and thus, fast-decomposing, compared to the stem component. This presumably facilitated faster release of allelochemical (s) stored in them. Several weeds have been reported to interfere with the growth and yield of crops through their allelopathic effects (Qasem and Foy 2001). The allelochemicals released by the weeds may enter the soil in various ways, e.g. leaching, root exudation and/ or through microbial decomposition of dead weed parts or through volatilization as in the aromatic plants. Thus, the phytotoxins in the soil may be contributed by residues through either of these processes. Amongst the crops, the maize shoot length compared to that of mung, showed relatively higher inhibitory impact of all four plant component residues. The residues of stem and reproductive

Table 2 Impact[1] of plant component residues[2] of *Ageratum conyzoides*: leaf (L), stem (S), reproductive part (RP) and root (R) on germination and shoot length (mean ± SE) of two crops, mung and maize in unamended (US) and amended soils

Treatment	Germination (%)		Germination speed		Shoot length (cm)	
	Mung	Maize	Mung	Maize	Mung	Maize
US	100	100	33.3	33.3	39.5±0.01a*	25.7±0.06a
L1	100 (nc)	100 (nc)	33.3 (nc)	33.3 (nc)	38.1±0.01f (-3.5)	22.5±0.05de (-12.5)
L3	67 (-33)	100 (nc)	18.8 (-43.5)	33.3 (nc)	36.6±0.03j (-7.5)	21.1±0.01e (-17.9)
L5	58 (-42)	100 (nc)	26.4 (-20.7)	33.3 (nc)	30.3±0.01m (-23.3)	19.1±0.01def (-25.8)
S1	100 (nc)	92 (-8)	33.3 (nc)	30.6 (-8.1)	38.7±0.02d (-2.1)	24.1±0.01bc (-6.2)
S3	100 (nc)	83 (-17)	27.8 (-16.5)	27.8 (-16.5)	37.5±0.01h (-5.2)	22.5±0.01d (-12.6)
S5	100 (nc)	75 (-25)	38.9 (-17)	25.0 (-24.9)	33.8±0.01l (-14.6)	21.9±0.01e (-14.8)
RP1	100 (nc)	83 (-17)	33.3 (nc)	27.8 (-16.5)	39.2±0.01c (-0.9)	26.8±0.99a (-0.4)
RP3	100 (nc)	75 (-25)	33.3 (nc)	25.0 (-24.9)	37.7±0.02g (-4.7)	24.3±0.01bce (-5.4)
RP5	75 (-25)	75 (-25)	20.8 (-37.5)	25.0 (-24.9)	35.4±0.01k (-10.5)	21.3±0.01e (-17.1)
R1	100 (nc)	83 (-17)	33.3 (nc)	27.8 (-16.5)	39.4±0.01b (-0.4)	23.6±0.01c (-8.2)
R3	83 (-17)	75 (-25)	20.8 (-37.5)	25.0 (-24.9)	38.3±0.01e (-3.1)	21.8±0.01e (-15.2)
R5	50 (-50)	50 (-50)	13.9 (-58.2)	16.7 (-49.8)	36.8±0.01i (-6.9)	19.2±0.01f (-25.3)

[1] Inhibition/stimulation over control (%) is given in the parentheses. [2] 1, 3 and 5 suffixed to the plant component codes indicate the amount of residue (g) added to 1 kg soil. * Values in the columns followed by the same letter(s) are not significantly different ($P < 0.05$) according to Duncan's test. nc= no change

parts had lesser impact compared to leaf and root. Roots are considered to comprise the major source of organic input in the soil and cause allelopathic effects through the release of an array of chemicals that are exuded into the rhizosphere that bring about considerable ecological effects (Bertin *et al*. 2003). Higher growth retardatory impact was recorded at higher dose (5g/kg). However, this growth inhibitory impact varied with plant component as well as with the type of crop. While the impact on mung was in the order $L_5>S_5>RP_5>R_5$, the growth retardatory impact on maize was in the order $L_5>R_5>RP_5>S_5$.

Table 3 Effect of plant component residues of *Ageratum conyzoides*: (leaf L, stem S, reproductive part RP and root R) on soil organic carbon (%) at 30 days after soil incorporation. US code indicates unamended/control soil

Residue source and amount (g)	Soil organic carbon		*p*
	Mean ± SE	% increase*	
US	0.68±0.003		< 0.001
L1	0.86±0.01	26.5	< 0.001
L3	0.91±0.01	33.8	< 0.001
L5	0.84±0.02	23.5	< 0.001
S1	0.76±0.02	11.8	< 0.001
S3	0.89±0.02	30.9	< 0.001
S5	0.85±0.01	25	< 0.001
RP1	0.69±0.01	1.5	ns
RP3	0.73±0.01	7.4	< 0.005
RP5	0.83±0.01	22.1	< 0.001
R1	0.79±0.01	16.2	< 0.001
R3	0.82±0.01	20.6	< 0.001
R5	0.93±0.01	36.8	< 0.001

The digits 1, 3 and 5 suffixed to the residue source codes (L, S, RP & R) indicate the weight in g/kg incorporated in soil. *P* values estimated by Dunnett's test. * % increase over control.

Phenolics, which are water-soluble allelochemicals have commonly been suggested to play a significant role in allelopathic interactions. Amadi *et al*. (2012) investigated the chemical profile of *Ageratum* using root, leaf, stem and reproductive parts. They have reported relatively higher amount of phenol, tannins, saponins, flavonoids and alkaloids in leaf compared to those found in other components. Flavonoids and tannins in stem and flower are reported to be relatively higher in concentration than those in the root. The observed growth-inhibitory influences could be attributed to higher concentrations of allelochemicals in these plant components, particularly in leaves and roots. Besides, they also comprised a larger proportion of fast-decomposing soft organic matter entering into the soil system after the death and decay of this seasonal weed.

Impact on soil organic carbon

A significant increase in soil organic C, in general, was recorded at the end of 30 days with the amendment of soil with different plant component residues of *Ageratum* (Table 3). The dose of 3 g residue showed higher stimulatory impact on the soil organic C compared to 1 g residue incorporated in 1 kg soil. However, 5 g residue had variable impacts on soil organic C in comparison to the impact of 3 g residues added to the soil. The leaf and stem residue showed an inhibitory impact whereas the root and reproductive part residues had stimulatory impacts.

Based on the results obtained, it is concluded that altered strategic differential biomass allocation pattern at newly intruded sites and potential release of phytotoxins especially by the soft leaf and root organs significantly contributed to the advancing expansion of this exotic invasive *Ageratum* in dry tropical anthropogenic regions of India.

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