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Aboveground Biomass Partitioning and Invasibility of *Sida acuta* Burm. f. in Indian dry Tropics

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Abstract

The pantropical malvaceous invasive weed Sida acuta Burm. f. was investigated for its varying morphological traits including its biomass allocation strategy to different above-ground organs at two contrasting sites: bank of polluted Kali river (KRB) and city-vegetation neighbouring the Ganga canal around Yamunapuram (YPM) in a peri-urban region in Indian dry tropics. Sixty plant individuals from each site at differing stage of their growth were clipped off from the base for the biomass measurements of their stem (stem-axis + branch), leaves and reproductive parts (flowers + capsules). The morphological traits studied were: shoot length, basal diameter and number of branches, leaves and flowers/capsules. Surface soil samples of both the study sites were analyzed for soil moisture, pH, organic C, available P and exchangeable K. S. acuta population at YPM site had significantly higher shoot length and stem-axis mass fraction. Biomass partitioning to different components was variable: stem (41-45%), leaf (47-52%) and reproductive parts (14-16%). Mean plasticity indices for plant-level traits were relatively higher at KRB site. Biomass of leaf, stem and reproductive parts was strongly correlated with total aboveground biomass. While leaf allocation declined significantly with plant size, stem allocation increased. Biomass allocation pattern of S. acuta populations did not show significant change with change of study sites in the present study, possibly due to comparable disturbance, soil and site conditions. In conclusion, invasiveness of this alien weed in peri-urban anthropo-ecosystems could be attributed mainly to its superior competitive ability manifested through higher allocation to photosynthetic and support organs.

Keywords: Peri-urban ecosystem, exotic, invasive, biomass allocation, phenotypic plasticity.

Introduction

Biological invasion is presently considered to be an important driver of global change. Invasion of native communities by exotic species, particularly the invasive ones, is recognized the world over as the second largest threat to biodiversity[1,2,3,4]. The tropics experience greater pressure of invasive species, as the process of plant species invasion gets accelerated with increased anthropogenic interventions[5]. The increasing human population and improved trans-continental transport have increased the scales of movement of non-native species. The current exacerbated rate of invasion constitutes one of the most important effects that humans have begun to witness on the earth ecosystem[6]. The ecological consequences of invasion by aliens have become an important global concern in light of their impact on alteration in the structure and function of the invaded ecosystems[7]. The ecosystem level consequences of invasion are, however, still little understood and there is an urgent need of studies on biological invasions in India[6], particularly in dry tropics that are rapidly facing urbanization-driven ecological modifications.

The urban and peri-urban ecosystems in Indian dry tropics have often been reported to harbour a large number of alien species which possibly followed the anthropogenic activities in this region[8]. The weedy vegetation in these anthropo-ecosystems has also been reported to be infested with many invasive/naturalized invaders[9]. The mosaic of vegetation, here, has *Parthenium hysterophorus*, *Ageratum conyzoides* and *Chenopodium murale* as the dominant alien invasives[10,11]. Despite the recognized dominating influence of the exotic alien species across diverse peri-urban anthropo-ecosystems[12,13], the information on invasive growth characteristics of the alien species is inadequate. Among them, the malvaceous weed *Sida acuta* Burm. f. is frequently seen in abundance across diverse land uses: degraded pastures, waste- and disturbed-places and roadsides[14,15]. This pantropical species is recognized as invasive alien weed in India[16,17,18]. Thus, this invasive species having annual-perennial life-form is likely to have high phenotypic plasticity that enabled it to successfully colonize in diverse alien environments. Compared with native species, the successful invasive species are generally reported to have greater stress tolerance and can thus acclimate to a larger range of environmental conditions[19,20]. Biomass allocation is often assumed as an important plant trait that allows the plants to optimize growth under varying soil scarce and growth stage conditions. An invasive plant species must be able to use fluctuating resources better[21], particularly in resource-scarce site conditions in and around urbanizing landscapes in peri-urban ecosystems[9]. Therefore, greater phenotypic plasticity is likely to confer greater vigour on invasive species[22,23,24]. Despite recognition of this weed's advancing abundance in dry tropics across a variety of habitat conditions, there exists little authentic information regarding biomass allocation pattern to its different organs that could be its important invasive characteristics, particularly in peri-urban areas in dry tropics.

The present work aimed at investigating the morphological traits and allocational plasticity of *Sida acuta* at two contrasting habitat conditions to understand its invasibility.

Material and Methods

Study area: The present study was carried out at Bulandshahr (28º04' and 28º43' N lat. and 77º08' and 78º28' E long.), located in the western part of Uttar Pradesh. The district is situated 237.44 m above sea level and lies in the Ganga and Yamuna Doab. The vegetation, here mainly comprised of mosaic of annual weeds and ruderals. The soil of the district includes broad belt of excellent alluvial soils formed from depositions by the Ganga and Yamuna river. The major developed cities around Bulandshahr, whose brunt of development it has faced, include Delhi (72 km), Noida (58 km), Meerut (69 km), Aligarh (69 km) and Ghaziabad (52 km) which are well connected with roads and railways. To accomplish the objectives of present study two study sites were selected. First study site was the bank of polluted Kali (black) river (KRB). This site witnessed the dumping of urban and sewage wastes. Agricultural fields, however, lay along its banks in the adjoining areas. The second site was the patches of vegetation around Yamunapuram colony (YPM) near Gang nahar canal. This site witnessed intensive transportation and human settlement activities interspersed with areas infested by weeds and ruderals. 1 km^2 area was selected at each site for intensive study.

The climate of the study area was semi-arid having three seasons: rainy, winter and summer. The monthly mean minimum temperature ranged from 8.0ºC (Jan) to 28.0ºC (Jun) and the mean maximum from 20.1ºC (Jan) to 41.5ºC (Jun). Annual mean rainfall was 642.3 mm having the maximum rainfall in the month of August (222.2 mm).

Soil analysis: Six representative surface-soil samples (0-10 cm) were randomly collected from each of the two study sites (KRB and YPM). The soil samples were air-dried and sieved (2 mm). Physico-chemical characteristics of soil samples were estimated that included soil-moisture content, pH, total organic carbon (Walkley and Black method)[25], available Phosphorous and exchangeable Potassium[26]. The other micro-nutrients estimated were: available S, Zn, Fe, Mn and Cu[25].

Plant-level measures: A total of one hundred and twenty individuals were randomly selected from two study sites (sixty each) at different stages of their growth (July – October) between 2008 and 2009. The selected individuals were carefully clipped off from the base at soil surface. Shoot length (SL) of the fresh individuals was measured from the shoot-top to bottom of the plant where the stem entered the soil. Basal diameter of all plant individuals was also measured. Plants were separated into different components, stem (stem-axis and branch), leaves and reproductive parts (flower and capsule). All plant components were then separately oven-dried at 80℃ for 48 h and weighed to the nearest 0.001 g to determine component biomass and above-ground biomass (AGB). The component mass fractions (stem-axis mass fraction, SAMF; branch mass fraction, BMF; stem (stem-axis + branches) mass fraction, SMF; leaf mass fraction, LMF and reproductive part (flowers + capsules) mass fraction, RPMF) were calculated as the biomass of each component in relation to the above-ground biomass.

Leaf area of 100 randomly selected fresh leaves from each site was measured by digital leaf area meter (Systronics).

Plasticity indices and Statistical analysis: The plant component mass fractions (SMF, LMF and RPMF) were studied in relation to total above-ground biomass (log scale). Biomass allometric relationships between each component mass fraction and total above-ground biomass were assessed through linear regression model[27]. Component mass fractions (SAMF, BMF, SMF, LMF and RPMF) were regressed against shoot length using second order polynomial regression model to determine the biomass allocation changes with increasing plant size.

The degree of plasticity among mature individuals (in reproductive phase) was compared by estimating the plasticity index (PI_v) for each trait[28]. The index extreme range includes zero (no plasticity) and one (maximum plasticity). It is evaluated as the difference between the maximum and minimum values of the trait divided by the maximum value at a site. The mean plasticity indices for plant-traits were evaluated for each species by averaging all variables.

Pearson product–moment correlation coefficients were generated to evaluate the linear association between traits and total above-ground biomass of plant individuals at both sites. The difference in the morphological traits of plants at two sites was statistically (SPSS 17.0) examined by t-tests (two tailed).

Results and Discussion

Plant level traits: Mean shoot length of sampled plant individuals was significantly higher ($p<0.05$) (table 1) at YPM site compared to KRB site. In contrast, BD/SL was higher at KRB site ($p<0.001$). On the mean basis, total number of branches, leaves, reproductive parts (flowers + capsules), biomass of stem-axis, branch, stem (stem axis + branch), leaf, reproductive parts and above-ground biomass were higher at YPM site, albeit the difference was not significant. The leaf biomass per leaf was significantly higher at YPM site ($p<0.05$). In terms of component mass fractions, the stem-axis mass fraction (SAMF) was significantly higher ($p<0.001$) at YPM site compared to KRB. While SMF was higher at YPM site, LMF was higher at KRB site, although the differences were not significant.

Table-1
Plant- and leaf-level traits (mean ± SE) of *Sida acuta* at Kali river bank (KRB) and Yamunapuram (YPM) study sites in a dry tropical peri-urban region

Traits	KRB	YPM	p value (t Test)
Shoot length (SL) (cm)	27.47 ± 2.91	38.97 ± 3.26	<0.05
Basal diameter (BD) (cm)	0.39 ± 0.04	0.39 ± 0.03	ns
BD/SL ratio	0.02 ± 0.001	0.01 ± 0.001	<0.001
Branch no.	14.23 ± 1.09	16.03 ± 1.17	ns
Total Leaf no.	165.2 ± 34.4	169.5 ± 31.8	ns
No. of rep parts (flowers + capsules)	245.4 ± 61.6	281.4 ± 56.5	ns
Stem-axis biomass (g)	1.31 ± 0.28	1.67 ± 0.33	ns
Branch biomass (g)	2.76 ± 0.81	2.98 ± 0.81	ns
Stem biomass (g)	2.92 ± 0.75	3.46 ± 0.84	ns
Leaf biomass (g)	1.17 ± 0.20	1.47 ± 0.26	ns
Single leaf biomass (g)	0.008 ± 0.001	0.011 ± 0.001	<0.05
Reproductive part biomass (g)	1.78 ± 0.53	2.11 ± 0.62	ns
Shoot biomass (AGB) (g)	4.95 ± 1.19	5.98 ± 1.37	ns
Stem-axis mass fraction (SAMF)	0.27 ± 0.01	0.33 ± 0.01	<0.001
Branch mass fraction (BMF)	0.23 ± 0.02	0.21 ± 0.02	ns
Stem mass fraction (SMF)	0.41 ± 0.02	0.45 ± 0.02	ns
Leaf mass fraction (LMF)	0.52 ± 0.03	0.47 ± 0.03	ns
Rep part mass fraction (RPMF)	0.14 ± 0.02	0.16 ± 0.03	ns
Leaf area (cm^2)	6.18 ± 0.57	6.35 ± 0.59	ns

Plasticity indices: The plasticity indices (PIv) of plant traits of *Sida acuta* ranged from 0.52 to 0.99 at KRB site and from 0.37 to 0.98 at YPM site (table 2). The mean plasticity was relatively higher at KRB site. Here, the plasticity indices for all plant traits (BD/SL ratio, SAMF, BMF, SMF and LMF) were higher compared to YPM site. RPMF, however, was much comparable at these two sites.

Pearson product correlation: Various plant traits, such as shoot length, basal diameter, number of branches, leaf and reproductive parts (flower + capsule), biomass of plant components (stem-axis, branch, leaf, reproductive part) were strongly and positively correlated with total above-ground biomass (AGB) of plants at both sites (KRB and YPM) (table 3). BD/SL ratio was positively related to AGB at KRB site while negatively related at YPM site although these relations were not significant. LMF was strongly and negatively correlated at both sites. On the other hand, SAMF showed negative and significant relation with AGB at YPM site only.

Table-2
Plasticity indices of different plant traits of *Sida acuta* at Kali river bank (KRB) and Yamunapuram (YPM) study sites in a dry tropical peri-urban region. Codes: BD basal diameter, SL shoot length

Plant-level traits	KRB	YPM
BD/SL ratio	0.73	0.50
Stem-axis mass fraction (SAMF)	0.75	0.61
Branch mass fraction (BMF)	0.91	0.89
Stem mass fraction (SMF)	0.52	0.37
Leaf mass fraction (LMF)	0.80	0.73
Rep part mass fraction (RPMF)	0.99	0.98
Mean	**0.78**	**0.68**

Table-3
Pearson product-moment correlation coefficient (r) for relationships between various plant-level traits and total above-ground biomass for *Sida acuta* at Kali river bank (KRB) and Yamunapuram (YPM) study sites in a peri-urban dry tropical region

Plant-level traits	KRB	YPM
Shoot length (SL) (cm)	.620**	.790**
Basal diameter (BD) (cm)	.773**	.801**
BD/SL ratio	0.026	-0.219
Branch no.	.448**	.598**
Total leaf no.	.969**	.899**
No. of rep part (flower + capsule)	.932**	0.901**
Stem-axis biomass (g)	.938**	.975**
Branch biomass (g)	.977**	.995**
Stem biomass (g)	.997**	.996**
Leaf biomass (g)	.879**	.919**
Single leaf biomass (g)	-0.153	-0.052
Reproductive part biomass (g)	.945**	.984**
Stem-axis mass fraction (SAMF)	-0.050	-.350**
Branch mass fraction (BMF)	.640**	.736**
Stem mass fraction (SMF)	.566**	.558**
Leaf mass fraction (LMF)	-.637**	-.644**
Rep part mass fraction (RPMF)	.392*	.558**

**Correlation is significant at the 0.01 level (2-tailed).
*Correlation is significant at the 0.05 level (2-tailed).

Allocation pattern: The SMF increased significantly with increasing plant size (AGB) (figure 1). However, at lower plant size, SMF was higher at YPM site compared to KRB site and the trend reversed at higher plant sizes. In contrast to increasing pattern of SMF, LMF declined significantly with increasing plant size (R^2 = 0.918 at KRB and 0.841 at YPM site). RPMF increased with plant size (R^2 = 0.211 at KRB and 0.470 at YPM site).

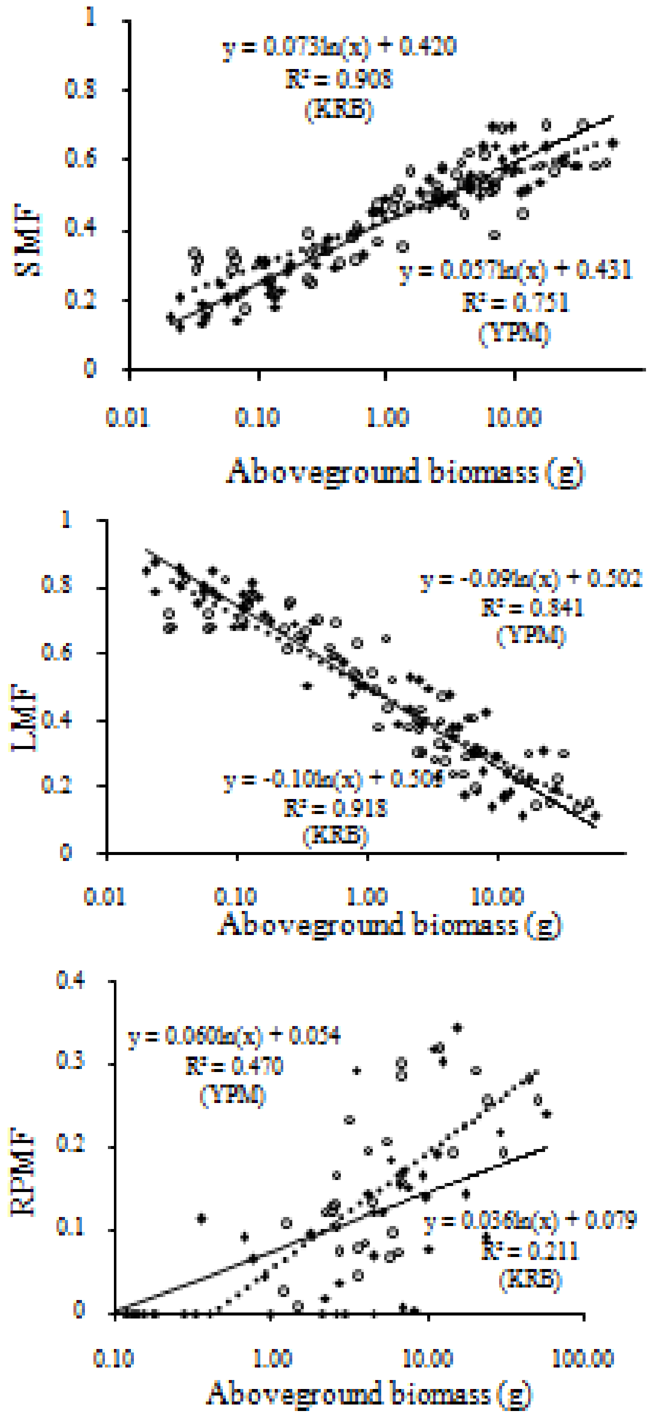

Figure-1

Allometric relationships between plant component mass fractions (stem mass fraction, SMF; leaf mass fraction, LMF and reproductive part mass fraction, RPMF) and total above-ground biomass (log scale) of *Sida acuta* at KRB site (filled squares and solid line) and YPM site (open circles and dotted line) in a dry tropical peri-urban region

Comparing the trends of organal mass fractions with increasing shoot length of *Sida acuta* at two different sites (figure 2), the LMF showed a significant and sharp decline at both sites (R^2 = 0.999 at KRB and 0.0.995 at YPM site) (table 4). A comparable trend for SAMF, BMF and SMF was recorded at both the sites. RPMF also showed an increasing trend with the maturity of the plant. The difference in the trends of allocation of biomass to different components was not found to vary significantly with change of study sites under the present investigation.

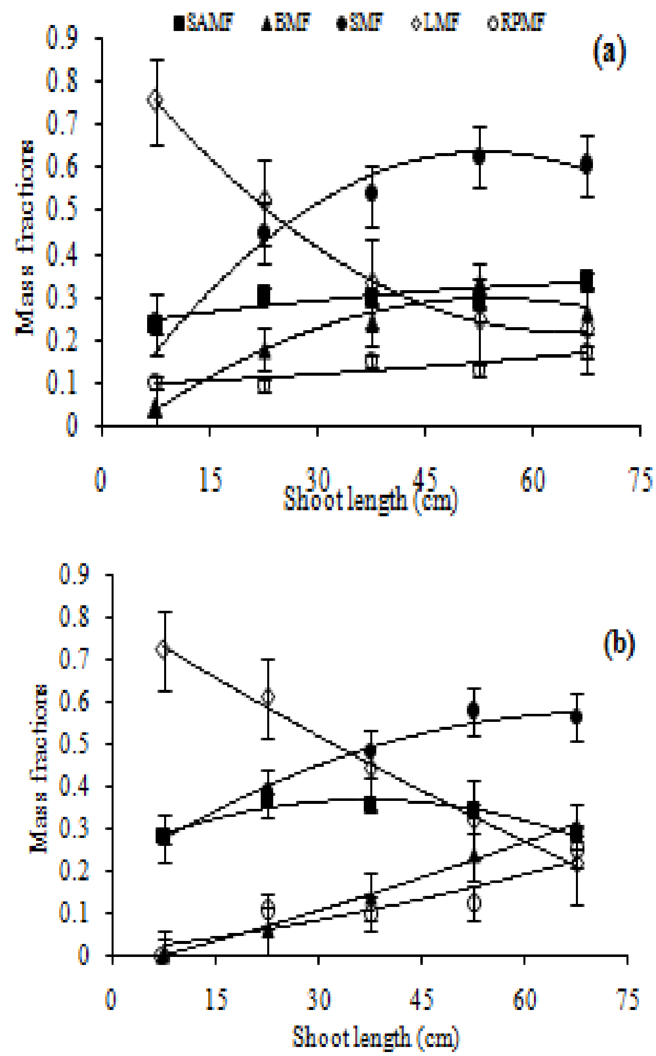

Figure-2

Variation of stem-axis mass fraction (SAMF), branch mass fraction (BMF), stem mass fraction (SMF), leaf mass fraction (LMF) and reproductive part mass fraction (RPMF) in relation to shoot length of *Sida acuta* at (a) Kali river bank (KRB) site and (b) Yamunapuram (YPM) site in a dry tropical peri-urban region. Curves represent best-fit second-order polynomial regression. Regression equations and R^2 values are presented in table 4.

Table-4
Regression equations and R^2 values of stem-axis mass fraction (SAMF), branch mass fraction (BMF), stem mass fraction (SMF), leaf mass fraction (LMF) and reproductive part mass fraction (RPMF) with shoot length of *Sida acuta* at Kali river bank (KRB) and Yamunapuram (YPM) study sites in a dry tropical peri-urban region, as presented in figure 2

Site	Regression equation	R^2 value
KRB	SAMF = $-0.003x^2 + 0.039x + 0.209$	0.744
	BMF = $-0.027x^2 + 0.222x - 0.160$	0.957
	SMF = $-0.033x^2 + 0.289x - 0.014$	0.991
	LMF = $0.037x^2 - 0.359x + 1.08$	0.999
	RPMF = $0.001x^2 + 0.008x + 0.087$	0.713
YPM	SAMF = $-0.020x^2 + 0.121x + 0.185$	0.906
	BMF = $0.002x^2 + 0.061x - 0.067$	0.995
	SMF = $-0.016x^2 + 0.176x + 0.111$	0.979
	LMF = $0.004x^2 - 0.157x + 0.882$	0.995
	RPMF = $0.004x^2 + 0.024x - 0.007$	0.857

Soil Characteristics: Soil moisture content (summer), organic carbon and other investigated soil nutrients were relatively higher in KRB soils compared to those in YPM soils (table 5) albeit statistically insignificant. Soil pH was however, significantly higher at YPM site ($p<0.01$).

Table-5
Physico-chemical characteristics of Kali river bank (KRB) and Yamunapuram (YPM) soils (mean ± SE) in a dry tropical peri-urban region

Soil Characteristics	KRB	YPM	p value (t Test)
Moisture content % (Summer)	0.89 ± 0.15	3.00 ± 0.92	ns
pH	6.86 ± 0.09	7.24 ± 0.05	<0.01
Org C	0.70 ± 0.08	0.54 ± 0.08	ns
Available P (Kg/ha)	18.43 ± 2.09	13.86 ± 1.99	ns
Exchangeable K (Kg/ha)	306.0 ± 11.5	241.0 ± 24.9	<0.05
Available S (ppm)	14.21 ± 0.53	13.45 ± 0.49	ns
Available Zn (ppm)	1.02 ± 0.10	0.93 ± 0.10	ns
Available Fe (ppm)	7.18 ± 0.46	6.93 ± 0.45	ns
Available Mn (ppm)	4.71 ± 0.13	4.63 ± 0.11	ns
Available Cu (ppm)	0.59 ± 0.04	0.58 ± 0.03	ns

Discussion: A significant alteration in biomass investment to different plant components with the change in developmental stage was revealed by the rainy annual *Sida acuta* in the present study. This recorded change could be attributed mainly to invasiveness and its tendency to perennial life form in the studied dry tropical peri-urban region. The biomass partitioned by this pantropical malvaceous weed to stem, although higher than the SMF reported for herbaceous species[29], was within the range (0.40-0.45) for five invasive herbaceous weeds in Indian dry tropics[8] (table 6). Amongst the support structural components, significantly greater stem-axis mass fraction (SAMF) of plants at YPM site compared to KRB site is possibly indicative of the fact that this weed invested more to its stem component for firm establishment to resist more frequent biotic interference at YPM site. However, the overall biomass partitioning to the stem was comparable at both the sites. The enhanced allocation to support structure indicated the growth strategy of this weed for strong establishment in this anthropic region. Considering allocation to three major above-ground components (leaf, stem and reproductive parts), the LMF in the present study at two sites (0.47-0.52) was much higher compared to LMF range reported for other weeds/herbs[8]. A significantly high allocation of biomass to leaves, indicative of investment to photosynthetic tissues, reflected the invasive character of this weed to outcompete the growth performance of native/alien weeds in this region[23,30,31,32]. Further, the invasion success for any exotic weed in the recourse-scarce peri-urban anthropo-ecosystems must depend upon the innate quality of weed roots to acquire the available soil nutrients. About 17% root allocation by *Sida acuta* in Indian peri-urban ecosystems has been reported[8]. A considerably high root allocation in resource-scarce sites in peri-urban anthropo-ecosystems, along with perennial growth tendency could be the major characteristics that contributed to the aggressiveness of this weed species here. The reproductive allocation by *Sida acuta* in this study, when compared with that by *Ageratum conyzoides* and *Chenopodium murale* (table 6), further corroborated the expansionist and invasive character of this weed in this region. Despite higher reproductive allocation the density of this weed appears constrained, as the number of seeds per plant varied from only 101 per plant[33] to 746 seeds/ plant recorded in this study.

Table-6
Comparison of biomass allocation values of different plant species, Allocation is characterized as a fraction of total biomass allocated to leaves (LMF), stems (SMF), roots (RMF) and reproductive parts (RPMF)

	SMF	LMF	RMF	RPMF
Herbaceous species[29]	0.24	0.46	0.3	-
Herbaceous weeds[8]	0.40-0.45	0.26-0.41	0.10-0.17	0.06-0.27
Chenopodium murale L.[9]	0.44-0.49	0.28-0.35	0.10-0.11	0.10-0.12
Ageratum conyzoides L.[10]	0.18-0.51	0.27-0.38	0.08-0.09	0.13-0.36
Sida acuta Burm. f.	0.41-0.45	0.47-0.52	-	0.14-0.16

Biomass allocation pattern reflected this weed's growth strategy to be establishment-centric. The invasive characteristic of *Sida acuta* appears to be greatly expressed through its differing stem characteristic at two study sites. Despite similar mean basal diameter, the mean shoot length was significantly higher at YPM site having relatively poor soil nutrients. Accordingly, BD/SL ratio was lower here. The higher shoot length allowed better light utilization potential and avoidance of shading by neighbouring plant species[34,35]. A considerable growth optimization ability of this invasive weed is documented by relatively higher total above-ground biomass at YPM compared to KRB site. However, the higher mean plasticity index at KRB site indicated greater plastic response to environmental variability here at highly polluted Kali river bank, as enhanced phenotypic plasticity is commonly suggested to play an important role in successful invasion of new habitats by alien species[36,37]. Amongst the three major above-ground components investigated here, the leaf allocation declined with plant size. On the other hand, stem and reproductive allocation increased. The initially higher leaf allocation in plants at younger stage of development is often suggested to meet the accelerated growth requirements, and it decreased with the maturity of the plants[38].

Despites the frequent occurrence of *Sida acuta* across various anthropo-ecosystems in the peri-urban region in Indian dry tropics[39], it has not been reported as the top leading dominant in any plant community amongst the vegetation mosaic here[12,39]. This could be attributed partially to its relatively poor ability to show pronounced differential biomass allocation pattern with the alteration in environmental conditions. This is evident from the present study, where insignificant alteration in the biomass allocation was observed across two study sites, albeit shift in the biomass partitioning to different components with ontogeny was clearly revealed in this study. However, variation in shoot biomass of *S. acuta* under the light/shade condition as well as in intra-specific competitive situations, has also been reported[40].

Conclusion

In conclusion, the invasiveness of *Sida acuta*, as evinced in the present study could be attributed to higher biomass allocation strategy to photosynthetic and support organs.

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