Spatio-temporal organization and biomass dynamics of plant communities in a dry tropical peri-urban region: deterministic role of alien flora in anthropo-ecosystems

Shachi Agrawal and Rup Narayan*

Department of Botany, I.P. (Post-Graduate) College, Bulandshahr 203 001, India

The species nativity, growth form, habit, invasion status, aboveground biomass (AGB) and belowground biomass (BGB) distribution and soil characteristics across six diverse habitat conditions were studied in a peri-urban region in Indian dry tropics to understand their deterministic impact on vegetation structure. Eighty-seven plant species, predominantly annuals (67%), belonging to 28 angiosperm families were recorded. Among them, 89% were exotics (largest of American and Asian origins) and 48% of the exotics were invasives while 16% were naturalized. AGB of annuals was higher than perennials, but the difference in their BGB was insignificant. Compared to natives, the exotics had higher AGB and BGB. Among them, the AGB species of South America, Asia and the Indian subcontinent had higher AGB, but the order was reversed in case of BGB. Similarly, AGB of invasives was higher than natives, but they showed comparable BGB. 'Non-native annual forbs' were the most dominant functional groups in terms of both AGB and BGB. The ordination results varied with plant BGB and AGB. Canonical correspondence analysis indicated dominant role of exotic invasives (mainly of American and European origin) and significant influence of soil organic carbon (SOC) and total nitrogen on vegetation organization. At lower SOC, AGB and BGB were comparable for both native and exotics. However, with the increase in SOC, native AGB and BGB declined, whereas AGB of non-native species increased. In conclusion, the study revealed large intrusion of alien floras into anthropo-ecosystems in Indian dry tropics, which significantly impacted structure and ecological processes both aboveground and belowground, as against better adaptation potential of the natives belowground.

Keywords: Aboveground and belowground biomass, alien flora, anthropo-ecosystems, exotics, peri-urban regions.

UNDERSTANDING the alteration in the structure of natural ecosystems under the synergistic impact of global environmental change and continued spread of non-native species will be an ecological challenge in the coming decades[1]. Thus investigations across diverse ecosystems, particularly the anthropo-ecosystems, which are the orderly combinations or arrangements of physical and biological environments built by man to sustain his kind have assumed considerable importance as they help comprehend the ways in which the real world diverges from the natural ideal one[2]. The inevitable consequence of habitat destruction here is to render ecosystems vulnerable to invasion by alien species that are transported intentionally or unintentionally by humans[3]. Invasion by such species often results in alterations in the functioning of invaded ecosystems[4]. Occurrence of such invasions is likely to be more apparent in and around urban landscapes with a variety of land uses that create an environment conducive for invading weeds[5,6]. Anthropo-ecosystems in such urban and peri-urban areas which represent hybrid landscapes of fragmented urban and rural regions created due to dispersive urban growth, are considered highly heterogeneous for plant survival and establishment[7,8]. These ecosystems have been disregarded by naturalists and conservationists for reportedly attracting cosmopolitan weedy flora that threaten the surrounding natural habitats[9].

Due to persistent anthropogenic pressure in the dry tropics, these areas have turned into low productive systems. Here, slow development of soil micro-flora makes these ecosystems highly fragile from the point of view of both structure and function. The spatial organization of such areas is usually unique[10]. Gradual conversion of such areas under urban sprawl leads to reduction in plant species diversity due to elimination of various important native ones, which is likely to facilitate acceleration in the abundance of competitively superior exotic species[5,6]. The productivity and nutrient availability in these ecosystems play a predominant role in determining plant community organization[11,12]. Between the native and alien species within a region, it is the latter which has often been suggested to adapt better to anthropogenic disturbances[13]. Differences between native and alien species

---

*For correspondence. (e-mail: rupnarayan2001@gmail.com) are likely to have important implications for understanding the aliens' interactions with, and effects on other species in a community. Biomass allocation patterns of plant species and communities are considered one of the most important aspects in their competitive life strategies for survival and expansion. They are significantly impacted by soil and site conditions, including the disturbance of past and present history there[14]. In spite of their importance particularly for peri-urban ecosystems which are adversely impacted by the increasing dominance of invasive weeds[7], ecological studies pertaining to the understanding of the community organization in terms of aboveground biomass (AGB) and belowground biomass (BGB) of plant species and community biomass relations with environment are lacking.

The present ecological study, carried out across various habitat conditions in a dry tropical peri-urban Indian region, aimed to investigate (i) species composition in terms of their biogeographic origin, invasion status and growth form, (ii) vegetation organization in terms of plant biomass, and (iii) native and non-native plant biomass relationship with soil characteristics.

Materials and methods

Study area

The present study was carried out at Bulandshahr (28°24′N lat. and 77°51′E long.), located in western Uttar Pradesh, India, at an altitude of ca. 180 m amsl. It is at the interface between urban and rural landscape. Since long it has been catering to the developmental needs of highly developed urban centres like Delhi, Noida, Gurgaon, Meerut and Ghaziabad. Developmental activities – planned or unplanned, in the last 5–6 decades have adversely impacted the vegetation structure and function here, and witnessed diverse land uses and anthropogenic activities.

Six study sites were selected in the National Capital Region of Delhi. These sites located within 3 sq. km area around the city covered contrasting land uses, viz. (1) grazing land (GL), (2) Kali river bank (KRB), (3) agricultural land (AL), (4) abandoned brick kiln (ABK), (5) Working brick kiln (WBK), and (6) intervening brick kiln (IBK). The GL site (basal cover area of vegetation 25–51 sq. cm/sq. m)[14] was located near a dairy milk industry. The KRB site (basal cover area of vegetation 39–43 sq. cm/sq. m)[14] was located along the banks of river Kali, a tributary of the Ganga. This river received untreated and partially treated industrial effluents and domestic sewage through heavily silted drains, besides urban dumps along the river bank. The AL site (basal cover area of vegetation 30–125 sq. cm/sq. m)[14], earlier occupied by a mango–guava orchard, witnessed shift to cereal and vegetable cultivation during the last 30 years. The ABK site (basal cover area of vegetation 51–53 sq. cm/sq. m)[14] was located around an abandoned brick kiln that witnessed active brick baking operations for 12 years at a large commercial scale and thereafter has been abandoned since the last five years. The WBK site (basal cover area of vegetation 28–40 sq. cm/sq. m)[14] was at a radial distance of 500 m from an abandoned brick klin and was actively operational for last five years. The IBK site (basal cover area of vegetation 25–35 sq. cm/sq. m)[14] lay intervening between these two sites. The soil of brick kiln sites was generally covered in varying degrees by brick dust and pieces of over-burnt and half-burnt bricks. At each site, 1–2 ha land was selected for the study.

The climate of the study area was semi-arid having three seasons – rainy (July–October), winter (November–February) and summer (March–June). The monthly mean minimum temperature ranged from 7.4°C (January) to 29.9°C (June), and the mean maximum from 16.5°C (January) to 39.7°C (June). Annual mean rainfall was 589 mm.

Species composition

Plant species were recorded from the monoliths excavated for biomass sampling across the six selected sites during the three seasons. They were identified[15,16] and the scientific nomenclature of these species was updated using taxonomic on-line databases such as The Annual Checklist of World Plants (http://www.sp2000.org) and E-Floras (http://www.efloras.org). Native geographical range of the plant species was obtained from Index Kewensis[17], specialized internet web pages (www.efloras.org) and some recently published similar studies[18–20]. In assigning the native ranges to all the species, a biogeographic approach was followed. Following Pysek *et al.*[21], the origin of the alien species was recognized at the continental scale, viz. Asia (excluding the Indian subcontinent), Europe, Africa, North America, South America and Australia. The species whose native ranges fell outside the borders of the Indian subcontinent were considered as non-native or alien. If a non-native species occurred in Asia as well as in other continent(s), then it was placed under Asia. The non-native species were categorized into five groups, viz. casual (Cs), naturalized (Nt), invasive (In)[8], casual or naturalized (C/N), and naturalized or invasive (N/I)[19]. The species whose invasion status could not be ascertained were placed under the 'unknown (Uk)' category.

Biomass sampling

The sampling of plant biomass across all six selected sites was carried out by excavating 30 monoliths (each to a depth of 20 cm) randomly at each site in February, June and October with the help of soil corer (inner diameter

22.6 cm, area ~400 sq. cm). They were washed carefully within 24 h of their extraction and the plant material collected on a 0.5 mm sieve, which was separated into different species to the extent possible. All plant individuals were fractioned into aboveground and belowground plant parts, including both live and standing dead parts. All aboveground and belowground plant parts were dried for 48 h at 80°C and weighed. Unidentified species were placed under miscellaneous category. The broken, unidentified belowground plant parts, which could not be linked to the aboveground parts, were also placed under miscellaneous category. Biomass (g m^{-2}) of aboveground and belowground parts was calculated for each of the species. The biomass data of all species and miscellaneous plant parts at a study site were pooled to obtain the total site biomass.

Soil analysis

Six representative surface soil samples (0–10 cm) were collected from each study site during each season. The soil samples were air-dried and sieved (2 mm). The soil moisture, pH, organic carbon (determined by Walkley and Black method) and total nitrogen (determined by micro-kjeldahl's method) were estimated following Piper[22]. Available phosphorus, exchangeable calcium and potassium of the soils were estimated following Allen *et al.*[23].

Data analysis

To examine the relationship between environmental variables and distribution of the species, a direct ordination with canonical correspondence analysis (CCA) was done using CANOCO 4.5 package[24]. CCA was performed using the biomass data of 87 plant species distributed across 18 vegetation stands (six study sites × three seasons) and eight environmental variables. The significance of the relationships was tested statistically by Monte Carlo permutation test using 999 unrestricted permutations.

Results

Species composition

A total of 87 plant species (20 grasses, 66 forbs and 1 fruit-tree seedling), predominantly annuals (67%) belonging to 28 angiosperm families were recorded across 6 sites in 3 seasons (18 vegetation stands) (Table 1). The largest families were Poaceae (17), Asteraceae (10), Amaranthaceae (8) and Malvaceae (7). Of the total recorded plant species, only 11% were native; the rest 89% were non-native. Among the non-native flora, 31% were of Asian origin, 30% South American, 22% European, 9% North American and 5% flora were of African origin. The rest 3% of the non-native flora were cryptogenic for their unknown origin. In terms of invasion status of the 77 alien flora recorded in the study, 48% were invasive, 16% naturalized, 10% naturalized or invasive, 5% casual or naturalized, 4% casual, 4% cultivated and 13% had unknown invasion status. The highest number of invasive species was recorded from Asteraceae (8), followed by Amaranthaceae (6) and Euphorbiaceae (3).

Biomass structure of native and non-native plant species across different sites and seasons

The species dominants changed with the change in their biomass data considered aboveground or belowground. In terms of AGB, the exotic invasive *Parthenium hysterophorus* was most dominant accounting for 11.9% of the plant biomass in the peri-urban area. It was followed by *Saccharum bengalense* (9.1%), *Chenopodium murale* (6.2%), *Senna obtusifolia* (5.9%), *Sida acuta* (5.9%) and *Achyranthes aspera* (5.2%). However, in terms of BGB, the native species *Cynodon dactylon* (14.9%) and *Saccharum bengalense* (13.9%) were the top dominants, followed by *Parthenium hysterophorus* (7.8%) and *Sida acuta* (5.5%).

BGB and AGB : BGB ratio of the plant species studied across different categories showed significant impact of growth form ($F_{2,354} \geq 5.568$, $P < 0.05$), habit ($F_{2,354} \geq 13.162$, $P < 0.001$), nativity ($F_{1,355} \geq 15.209$, $P > 0.001$), biogeographic region of origin ($F_{6,350} \geq 5.751$, $P < 0.001$), invasion status ($F_{7,349} \geq 3.534$, $P \leq 0.001$) and functional group ($F_{11,345} \geq 5.953$, $P < 0.001$) of the species. Amongst the growth forms, annuals showed significantly higher AGB (283.71 g m^{-2}) compared to perennials (98.25 g m^{-2}), and annual to perennials (58.42 g m^{-2}) (Table 2). However, in terms of BGB, difference between annuals and perennials was insignificant. The AGB of forbs was significantly higher compared to grasses. Non-native species showed significantly higher AGB and BGB compared to native species in this study.

The AGB occupied by plant species in terms of their origin in different continents was in the order: South America > Asia > Indian subcontinent > North America > Europe > Africa, whereas BGB occupancy was in the order: Indian subcontinent > Asia > South America > Europe > North America > Africa (Table 2). AGB of invasive species was significantly higher than that of species groups of other invasion status. BGB of invasive species was comparable to the native ones. Amongst the functional groups, 'non-native annual forb' was the most dominant group in terms of both AGB and BGB. Comparing AGB : BGB (shoot : root) ratio, invasives had much higher value (4.1) compared to native species (1.6). This ratio amongst species of different biogeographic origins was recorded lowest for those of the Indian

Table 1. Plant species recorded across the six studied sites in three seasons in a dry tropical peri-urban area

Species	Abbreviation	Family	Type	Growth form	Native/ non-native	Native region	Invasion status
Abutilon indicum (L.) Sweet	*Abu ind*	Malvaceae	Forb	A–P	nn	Tropical Geront	Uk
Achyranthes aspera L.	*Ach asp*	Amaranthaceae	Forb	A–P	nn	Tropical America	In
Ageratum conyzoides L.	*Age con*	Asteraceae	Forb	A	nn	South America	In
Alternanthera pungens Kunth.	*Alt pun*	Amaranthaceae	Forb	P	nn	Tropical America	In
Alternanthera sessilis (L.) R. Br. ex DC.	*Alt ses*	Amaranthaceae	Forb	P	nn	Tropical America	In
Amaranthus spinosus L.	*Ama spi*	Amaranthaceae	Forb	P	nn	Tropical America	In
Amaranthus viridis L.	*Ama vir*	Amaranthaceae	Forb	A	nn	Pantropical	C/N
Anagallis arvensis L.	*Ana arv*	Primulaceae	Forb	A	nn	Mediterranean Europe	In
Anisomeles indica (L.) Kuntze	*Ani ind*	Lamiaceae	Forb	A–P	n	Oriental India, Malaya	N
Argemone mexicana L.	*Arg max*	Papaveraceae	Forb	A	nn	West Indies	In
Blumea lacera (Burm. f.) DC.	*Blu lac*	Asteraceae	Forb	A	nn	Tropical America	In
Boerhavia diffusa L.	*Boe dif*	Nyctaginaceae	Forb	P	nn	Cryptogenic	N/I
Bothriochloa pertusa A. Camus	*Bot per*	Poaceae	Grass	P	nn	Asia (excluding the Indian sub-continent), Africa	Nt
Brassica campestris L.	*Bra cam*	Brassicaceae	Forb	A	nn	Europe	Cs
Cannabis sativa L.	*Can sat*	Cannabinaceae	Forb	A–P	nn	Central Asia	In
Senna obtusifolia (L.) H.S. Irwin & Barneby	*Sen obt*	Caesalpinaceae	Forb	A	nn	Tropical America	In
Senna occidentalis (L.) Link	*Sen occ*	Caesalpinaceae	Forb	A	nn	South America	In
Celsia coromandeliana Vahl	*Cel cor*	Scrophulariaceae	Forb	A	n	Oriental India, Afghanistan	N
Chenopodium album L.	*Che alb*	Chenopodiaceae	Forb	A	nn	Paleotropical	In
Chenopodium ambrosioides L.	*Che amb*	Chenopodiaceae	Forb	A	nn	South America	Nt
Chenopodium murale L.	*Che mur*	Chenopodiaceae	Forb	A	nn	Africa, Europe	Nt
Cirsium arvense (L.) Scop.	*Cir arv*	Asteraceae	Forb	A	nn	Asia (excluding the Indian sub-continent)	In
Commelina benghalensis L.	*Com ben*	Commelinaceae	Forb	A	nn	Tropical Geront	Uk
Corchorus aestuans L.	*Cor aes*	Tiliaceae	Forb	A	nn	Tropical America	In
Croton bonplandianum Baill.	*Cro bon*	Euphorbiaceae	Forb	A	nn	South America	In
Cynodon dactylon (L.) Persoon	*Cyn dac*	Poaceae	Grass	P	n	Cosmopolitan	N
Cyperus rotundus L.	*Cyp rot*	Cyperaceae	Grass	P	nn	Pantropical	In
Dactyloctenium aegyptium (L.) P. Beauv.	*Dac aeg*	Poaceae	Grass	A	nn	Pantropical	N/I
Dichanthium annulatum (Forsk.) Stapf	*Dic ann*	Poaceae	Grass	P	nn	Tropical Africa	Uk
Digera muricata Mart.	*Dig mur*	Amaranthaceae	Forb	A	nn	North America	In
Digitaria adscendens Hern.	*Dig ads*	Poaceae	Grass	A	nn	Asia (excluding the Indian sub-continent), Africa	Cs
Alternanthera paronychioides St. Hil.	*Alt par*	Amaranthaceae	Forb	P	nn	South America and West Indies	In
Eleusine coracana Gaertn.	*Ele cor*	Poaceae	Grass	A	nn	Eastern Africa	Cl
Eragrostis ciliaris (Linn.) R.Br.	*Era cil*	Poaceae	Grass	A	nn	Tropical America	Uk
Euphorbia hirta L.	*Eup hir*	Euphorbiaceae	Forb	A	nn	Tropical America	In
Euphorbia thymifolia L.	*Eup thy*	Euphorbiaceae	Forb	A	nn	Tropical America	In
Fimbristylis dichotoma Vahl.	*Fim dic*	Cyperaceae	Grass	A–P	nn	Asia (excluding the Indian sub-continent), Africa	Nt
Fumaria indica Pugsley	*Fum ind*	Fumariaceae	Forb	A	nn	Temperate northern Asia	N/I
Gnaphalium pensylvanicum Willd.	*Gna pen*	Asteraceae	Forb	A	nn	North America	In
Gomphrena celosioides Mart.	*Gom cel*	Amaranthaceae	Forb	A–P	nn	South America	N/I
Lathyrus odoratus L.	*Lat odo*	Papilionaceae	Forb	A	nn	Mediterranean Europe	Nt
Launaea asplenifolia (Willd.) Hook. F.	*Lau asp*	Asteraceae	Forb	A–P	n	Oriental India	N
Leptochloa panicea (Retz.) Ohwi	*Lep pan*	Poaceae	Grass	A	nn	Northern America	Uk
Lycopersican esculantum Mill.	*Lyc esc*	Solanaceae	Forb	A	nn	South America	Cs
Malva parviflora L.	*Mal par*	Malvaceae	Forb	A	nn	Southern Europe	N/I
Malvastrum coromandelianum Gracke	*Mal cor*	Malvaceae	Forb	A	nn	West Indies	In
Medicago sativa L.	*Med sat*	Papilionaceae	Forb	A–P	nn	Caucasus &West Asia	C/N
Melilotus indicus (L.) All.	*Mel ind*	Papilionaceae	Forb	A	nn	Europe, West Asia	Nt
Ocimum americanum L.	*Oci amer*	Lamiaceae	Forb	A	nn	Tropical Africa	In
Oplismenus burmannii (Retz.) P. Beauv.	*Opl bur*	Poaceae	Grass	A	n	Tropical Amphigea	N
Oxalis corniculata L.	*Oxa cor*	Oxalidaceae	Forb	A–P	nn	Europe	In
Panicum miliaceum L.	*Pan mil*	Poaceae	Grass	A	nn	Asia (excluding the Indian sub-continent)	C/N

(Contd)

Table 1. (*Contd*)

Species	Abbreviation	Family	Type	Growth form	Native/ non-native	Native region	Invasion status
Parthenium hysterophorus L.	*Par hys*	Asteraceae	Forb	A	nn	Central America	In
Paspalidium flavidum (Retz.) A. Camus	*Pas fla*	Poaceae	Grass	A–P	n	Africa, Asia Temperate, Asia Tropical, Australia, Pacific	N
Peristrophe paniculata (Forssk.) Brummitt	*Per pan*	Acanthaceae	Forb	A–P	nn	Tropical America	In
Phalaris minor Retz.	*Pha min*	Poaceae	Grass	A	nn	Mediterranean region	In
Phyllanthus fraternus Webster	*Phy fra*	Euphorbiaceae	Forb	A	n	Tropical Asia	N
Physalis angulata L.	*Phy ang*	Solanaceae	Forb	A	nn	America	In
Poa annua L.	*Poa ann*	Poaceae	Grass	A	nn	Europe	Nt
Polygonum plebejum R.Br.	*Pol ple*	Polygonaceae	Forb	A–P	nn	Tropical and Temperate Geront	Uk
Psidium guajava L.	*Psi gua*	Myrtaceae	Tree	P	nn	Tropical America	Nt
Ranunculus sceleratus L.	*Ran sce*	Rannunculaceae	Forb	A	nn	Europe	Nt
Rumex dentatus L.	*Rum den*	Polygonaceae	Forb	A	nn	Africa, Europe	Nt
Saccharum bengalense Retz.	*Sac ben*	Poaceae	Grass	P	n	Temperate & Tropical Asia	N
Scirpus articulatus L.	*Sci art*	Cyperaceae	Grass	A–P	n	Oriental India	N
Coronopus didymus Sm.	*cor did*	Brassicaceae	Forb	A	nn	Tropical America	In
Setaria glauca (L.) P. Beauv.	*Set gla*	Poaceae	Grass	A	nn	Europe, Temperate Asia	Uk
Sida acuta Burm. f.	*Sid acu*	Malvaceae	Forb	A	nn	Pantropical	In
Sida cordifolia L.	*Sid cor*	Malvaceae	Forb	P	nn	Pantropical	N/I
Sida rhombifolia L.	*Sid rho*	Malvaceae	Forb	A	nn	Pantropical	N/I
Silene conoidea L.	*Sil con*	Caryophyllaceae	Forb	A	nn	Temperate Eurasia	N/I
Sisymbrium irio L.	*Sis iri*	Brassicaceae	Forb	A	nn	Europe, Boreal Asia and Africa	Uk
Solanum nigrum L.	*Sol nig*	Solanaceae	Forb	A–P	nn	Europe, Northern Africa and West Asia	In
Sonchus asper Hill	*Son asp*	Asteraceae	Forb	A	nn	Mediterranean Europe	In
Spergula arvensis L.	*Spe arv*	Caryophyllaceae	Forb	A	nn	Europe	In
Stellaria media Vill.	*Ste med*	Caryophyllaceae	Forb	A	nn	Europe	Nt
Trianthema portulacastrum L.	*Tri por*	Aizoaceae	Forb	A	nn	Tropical America	Uk
Tribulus terrestris L.	*Tri ter*	Zygophyllaceae	Forb	A	nn	Pantropical	In
Tridax procumbens L.	*Tri pro*	Asteraceae	Forb	A–P	nn	Mexico	In
Trifolium alexandrinum L.	*Tri ale*	Papilionaceae	Forb	A	nn	West Asia and Asia Minor	C/N
Triticum aestivum L.	*Tri aes*	Poaceae	Grass	A	nn	na	Cl
Urena lobata L.	*Ure lob*	Malvaceae	Forb	A–P	nn	Tropical Africa	In
Vernonia cineria Less.	*Ver cin*	Asteraceae	Forb	A–P	nn	Tropical Amphigea	Uk
Veronica anagallis-aquatica L.	*Ver ana*	Scrophulariaceae	Forb	A	nn	Temperate Eurasia	Nt
Vigna radiate	*Vig rad*	Papilionaceae	Forb	A	n	Pantropical	N
Xanthium strumarium L.	*Xan str*	Asteraceae	Forb	A	nn	South America	In
Zea mays L.	*Zea may*	Poaceae	Grass	A	nn	Central America	Cl

Species abbreviated name, family, type (grass/forb), growth form (A, annual; P, perennial), nativity (n, native; nn, nonnative), native region and invasion status (Cl, cultivated; Cs, casual; C/N, casual/naturalized; Nt, Naturalized; N/I, naturalized/invasive; In, invasive; Uk, unknown) are also shown.

subcontinent (1.57), which was much lower than the plant species of American origin (about 5). The native species also showed lower ratio (1.6) compared to non-native ones (3.7).

CCA ordination

The proportion of variance of species data and species–environment relationships explained by all four CCA axes were relatively comparable for both AGB and BGB data of the species, although the values were higher for BGB. The four CCA axes explained >73% of species–environment variance (Table 3). In these CCA ordinations (Figure 1 shown for AGB of plant communities), the Monte Carlo permutation test indicated significant eigenvalues for all canonical axes examined ($P < 0.01$). The results indicated that CCA analyses performed well in describing the relationships between vegetation and environmental variables[24,25] and this performance was better for BGB.

The ordination of vegetation stands differed when analysed in terms of BGB and AGB of plant species comprising them. Their distribution varied considerably in their response to soil characteristics, viz. organic C, total N, C : N ratio, pH, available P, exchangeable K and Ca. The first CCA axis was strongly and negatively correlated with soil organic carbon/SOC and C : N ratio (Table 3). The vegetation stands at brick kiln sites with

Table 2. Aboveground and belowground biomass (mean value) of species belonging to different categories of growth form, habit, nativity, biogeographic region of origin, invasion status and functional group in an Indian dry tropical peri-urban region

Plant species category	Aboveground biomass (g m^{-2})	Belowground biomass (g m^{-2})
Growth form		
Annual	283.71 a	72.73 a
Perennial	98.25 b	59.03 a
Annual to perennial	58.42 b	13.58 b
Habit		
Grass	110.94 a	68.91 a
Forb	329.43 b	76.42 a
Nativity		
Native	74.47 a	47.55 a
Non-native	365.92 b	97.78 b
Biogeographic region of origin		
Indian sub-continent	74.47 ab	47.55 b
Asia (excluding Indian subcontinent)	84.31 ab	29.76 ab
South America	120.51 b	25.16 ab
North America	72.17 ab	14.71 a
Europe	66.90 ab	19.04 ab
Africa	6.72 a	2.25 a
Cryptogenic	15.32 ab	6.87 ab
Invasion status		
Cultivated	18.34 a	5.74 abc
Casual	1.65 a	0.74 a
Casual/naturalized	2.10 a	0.32
Naturalized	42.60 a	10.95 ab
Naturalized/invasive	46.55 a	16.24 abc
Invasive	233.00 b	57.32 c
Unknown	21.68 a	6.47 ab
Native	74.47 a	47.55 bc
Functional groups		
Native annual grass	0.69 ab	0.14 a
Native annual forb	5.51 ab	1.20 a
Native perennial grass	61.25 b	42.41 b
Native perennial forb	-	-
Native annual to perennial grass	5.64 ab	3.31 a
Native annual to perennial forb	1.38 a	0.50 a
Non-native annual grass	36.00 a	15.38 a
Non-native annual forb	241.52 a	56.00 a
Non-native perennial grass	7.20 a	7.53 a
Non-native perennial forb	29.78 ab	9.09 a
Non-native annual to perennial grass	0.16 ab	0.13 a
Non-native annual to perennial forb	51.25 ab	9.64 a

In each category, mean values with common letters are not significantly different at $P \leq 0.05$ according to Tukey's HSD test.

lower soil nutrients ordinated towards the right and those at grazing land site towards the left which had relatively higher SOC (Figure 1). The second CCA axis was most strongly correlated with pH and moderately associated with available P (Table 3). The third CCA axis, however, showed strong and significant relationships with SOC, C : N ratio, moisture, available P, exchangeable Ca and K. The ordination results thus indicated considerable influence of soil characteristics on the organization of vegetation stands. The dispersion of stands, as visualized, was maximum in winter and least during rainy season, reflecting that seasonality plays an important role in community organization here. The species and vegetation stands in the studied area were scattered over the available space, except clusters of species in agricultural land during winter and summer seasons. At this site, crop species along with its associated weed competitors formed distinct patches on the upper side of the *X*-axis. Species like *Saccharum bengalense*, *Euphorbia hirta*, *Launea asplenifolia* and *Urena lobata* ordinated towards the right side of the *Y*-axis at the low-nutrient sites (Figure 1).

With increasing SOC, native and non-native species showed contrasting trends in terms of both AGB and BGB (Figure 2). At lower SOC both native and

Table 3. Results of canonical correspondence analysis, relative abundances (in terms of aboveground biomass) of 87 plant species to 8 environmental variables at 18 vegetation stands in the peri-urban region in Indian dry tropics

Axis	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.660	0.614	0.539	0.363
Species–environment correlations	0.953	0.880	0.907	0.893
Cumulative percentage variance				
Species data	12.6	24.3	34.5	41.4
Species–environment relation	22.2	42.8	60.9	73.1
Inter-set correlations of environmental variables				
Moisture	–0.2098	0.2070	–0.5364*	0.0865
pH	0.2387	0.6160**	0.0872	0.1447
Organic C	–0.4621*	–0.1480	0.5489*	–0.0217
Total N	–0.2632	–0.2061	0.3813	–0.3385
C : N ratio	–0.4992*	0.0854	0.4753*	0.2454
Available P	–0.2740	0.4147	0.6272**	0.3573
Exchangeable K	0.1246	0.2428	0.5530*	–0.5314*
Exchangeable Ca	0.3351	–0.2129	0.6158**	0.2163

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

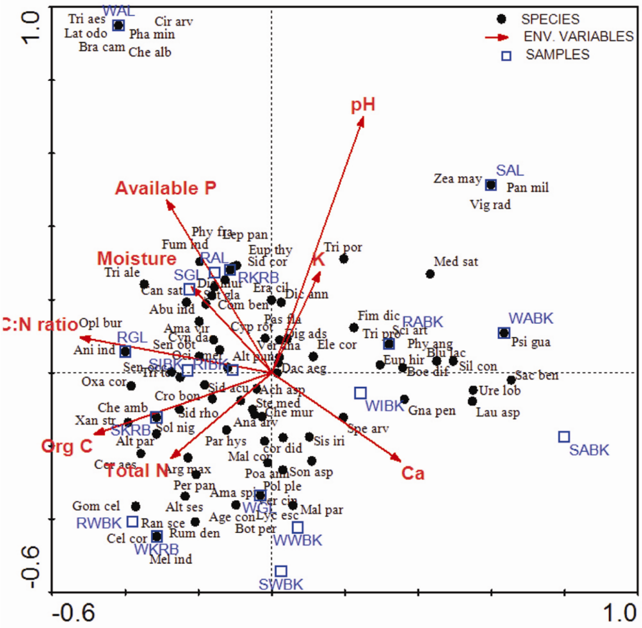

Figure 1. Canonical correspondence analysis ordination of 18 vegetation stands with 8 environmental variables. For stand codes, the first letter indicates season (R, rainy; W, winter; S, summer) and next 2–3 letters indicate site name (GL, grazing land; KRB, Kali river bank; AL, agricultural land; ABK, abandoned brick kiln; IBK, intervening brick kiln; WBK, working brick kiln). For species abbreviation refer to Table 1.

non-native species tended to have comparable AGB and BGB. However, with increasing SOC, both AGB and BGB declined significantly for native species. In contrast, AGB of non-native species increased significantly ($P < 0.05$).

Discussion

A large-scale intrusion by alien flora (89%) in this study, against intrusion by 40% exotics reported at the country level[26], indicates high vulnerability of the investigated region. This may be considered reflective of the higher response of aliens over the natives to warm, urbanizing, low-altitude, peri-urban areas[27], and increasing impact of human activities and movement in this region that facilitated arrival and gradual establishment, and later, naturalization and spread[28] of the exotics. Further, perhaps because of the long history of agriculture and connections with other regions through heavy vehicular transportation, not much of the native plant populations are left. Almost nothing of the native flora is left in the vast Gangetic Plain to start restoration. The largest representation of floras of American origin (39%) in this study and the whole country in general, can be attributed to the increase in international trade between Asia and America, as well as their biogeographical affinities[29,30]. Under comparable conditions, the largest number of alien floras of American origin has also been reported in China[31].

The weedy species, in this study, belonging largely to Poaceae, Asteraceae, Amaranthaceae, Malvaceae and Papilionaceae, accounted for 47% of the total non-native flora (77) recorded. These angiosperm families have also been the major contributors to the alien flora, not only in Asian cities and regions, but also worldwide[31–35]. Among these exotics, the highest number of invasives belonged to Asteraceae, Amaranthaceae and Euphorbiaceae, which are reportedly abundant in tropical or warm climate[31]. Occurrence of 48% invasives, 16% naturalized, 10% naturalized or invasive in this study, against that reported at the country level (14%, 16% and 8% respectively)[19], indicated considerable transformation of exotics into invasives in the studied region, e.g. *Chenopodium murale* has recently been recognized as an aggressive botanical invader in this region[36].

Preponderance of annuals (67%) may be driven by a variety of agricultural and other anthropogenic activities[30,37]. These annuals are more plastic compared to perennials, with the ability to invade a larger geographical area[38,39]. They showed significantly higher AGB compared to perennials and other growth forms (Table 2). However, in terms of BGB, insignificant difference between annuals and perennials was indicative of high growth optimization ability of the annuals[40]. In fact, the annual growth form can be considered by far the most predominant life strategy of both the naturalized and invasive plant species. Among the functional groups, non-native annual forbs with higher AGB as well as BGB, reflected better resource utilizing ability of these intruded non-native annual flora, especially the forbs.

The spatio-temporal dynamics of the investigated weed communities is evident from the dispersion of vegetation stands (Figure 1). Reduced discreteness of vegetation patches, generally in the rainy season, could be due to homogenization impact of adequate moisture availability in the dry tropical soils. This presumably enabled different kinds of propagules (present locally or transport-propagated) to grow and mature. Accordingly, the diverse ecosystems in this region witnessed the highest diversity in the rainy season[41].

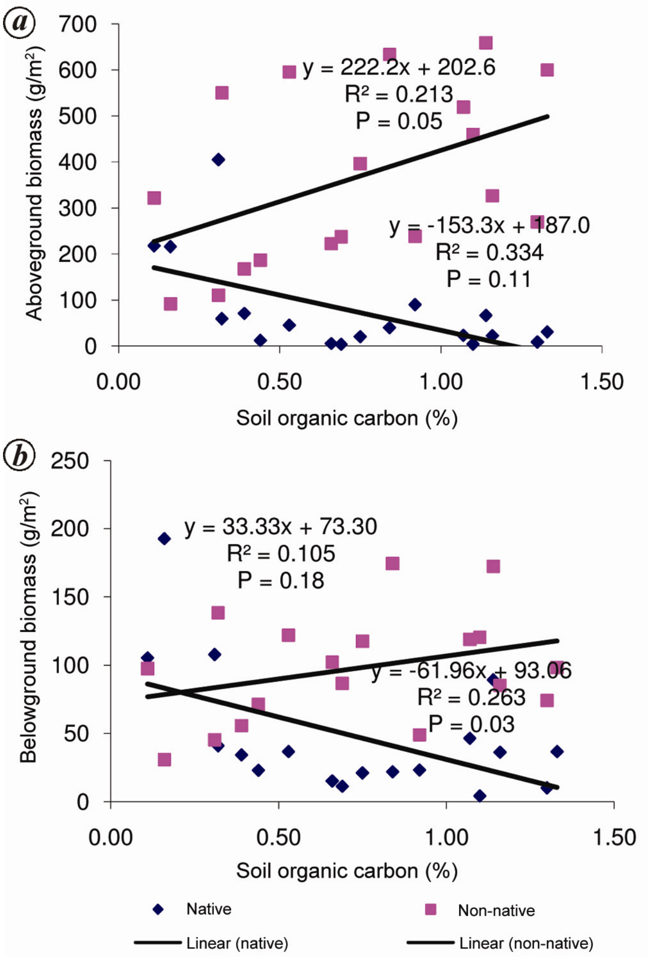

Figure 2. Variation of (***a***) aboveground and (***b***) belowground biomass of native and non-native species with increasing soil organic carbon.

The spatial organization of vegetation stands and the species assemblages were also influenced by SOC and total N, despite relatively poor soil nutrients[14]. The vegetation stands under resource-scarce states at the brick kiln sites (low soil moisture, organic C and total N)[42] ordinated in contrast to those at grazing land sites having relatively high resource-rich soils[41] (Figure 2). The distinctness of the much disturbed and nutrient-poor ABK site owed much to the dominance of native perennial forb *Saccharum bengalense* that sustained resource-scarce soils by investing greater biomass to roots (its BGB being 13.8% and AGB being 11.3% at the regional level). Investment to roots meant increased nutrient-absorption organs[43].

The heterogeneity of the vegetation patches, as evinced in this study, discernible even at lower spatial scale, suggested complex vegetation structure in the peri-urban areas. Human or anthropogenic activities created open spaces that were largely occupied by alien annual flora (as ecological opportunists). Further operation of diverse disturbance regimes (brick kiln activities, carrying of pollution load by Kali River, etc.) and land-use changes added to the environmental complexity. It is well known that after disturbance, resources and colonization opportunities are greatly elevated, thus making the disturbed areas most susceptible to invasion. This trend is further accentuated by human-mediated propagule dispersal (transport-associated)[44].

The plant species largely native to America (South and North) and Europe, and SOC and total N vectors (the major deterministic environmental variables) (Figure 1), may be considered as suggesting that the organization and productivity of plant communities in this study, were much influenced by the botanical invaders from these continents. Thus, pointing to the deterministic role of such alien flora with the potential to cause landscape-scale alterations by affecting organisms and ecological processes both aboveground and belowground.

Broadly, the subterranean biomass build-up (BGB) and differential allocation to aboveground and belowground plant parts (AGB : BGB ratio) in this study were significantly influenced by growth forms, habit, nativity, biogeographic region of origin and invasion status of the plant species. The non-native plant species differently allocated higher AGB (higher AGB : BGB, indicative of better utilization of aboveground resources, e.g. light and CO_2, etc.)[45]. The Indian native species, on the other hand, appeared to resist and contest competitively with the invaders, especially under edaphic stress conditions through their enhanced belowground allocation (lower AGB : BGB ratio for better acquisition of belowground resources, e.g. water and soil nutrients)[43]. The present investigation exhibited the highest AGB as well as AGB : BGB ratio in the alien species of South American origin. In contrast, the native Indian subcontinental flora had the highest BGB and lower AGB : BGB ratio. Two major natives *Cynodon dactylon* and *Saccharum bengalense* were the top dominants accounting for about 30% of the total BGB in the study area. In contrast, the combined BGB contribution by two most prominent non-native weeds, *Parthenium hysterophorus* and *Sida acuta* was less than half of these two natives. Thus, the alien species showed better adaptation to anthropogenic disturbance. This is further evident from the success of the invasive species with much higher AGB than the natives and species groups of other invasion status, and BGB comparable to that of the native species.

The negative correlation observed between SOC and BGB across these peri-urban habitats is indicative of an adaptation strategy to maximize growth and fitness conditions[46]. In the present study, the contrasting trends of BGB and AGB of native and non-native species along soil fertility gradient indicated that the latter species with higher biomass at nutrient-rich sites, efficiently utilized the soil resources for their growth, and performed equally well under resource-scarce soil conditions. This allocation strategy clearly explained that plasticity of invasive species increased their ability to spread to a wide range of habitats with resource variability.

In conclusion, this study revealed high-scale invasion by exotic flora and their considerable influence on community organization and productivity in the peri-urban ecosystems in Indian dry tropics, and the potential of these plants to impact organisms and ecological processes, both aboveground and belowground. The non-native plants adapted better to dry and sterile conditions, through enhanced growth, both above- and below-ground, in contrast to the natives optimizing their growth through enhanced belowground allocation.

---

1. Drenovsky, R. E. *et al.*, A functional trait perspective on plant invasion. *Ann. Bot.*, 2012, doi:10.1093/aob/mcs100.
2. Santos, M. A. and Filho, W. L., An analysis of the relationship between sustainable development and the anthroposystem concept. *Int. J. Environ. Sustain. Dev.*, 2005, **4**(1), 78–87.
3. Moore, P. D., Alien invaders. *Nature*, 2000, **403**, 492–493.
4. Mack, R. N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M. and Bazzaz, F. A., Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.*, 2000, **10**(3), 689–710.
5. McKinney, M. L., Urbanization, biodiversity, and conservation. *BioScience*, 2002, **52**(10), 883–890.
6. Turner, W. R., Nakamura, T. and Dinetti, M., Global urbanization and the separation of humans from nature. *BioScience*, 2004, **54**(6), 585–590.
7. Gupta, S. and Narayan, R., Plant diversity and dry-matter dynamics of peri-urban plant communities in an Indian dry tropical region. *Ecol. Res.*, 2011, **26**(1), 67–78.
8. Pyšek, P., Richardson, D. M., Rejmánek, M., Webster, G. L., Williamson, M. and Kirschner, J., Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, 2004, **53**(1), 131–143.
9. Turner, K., Lefler, B. and Freedman, B., Plant communities of selected urbanized areas of Halifax, Nova Scotia, Canada. *Landsc. Urban Plan*, 2005, **71**, 191–206.
10. Sukopp, H., On the early history of urban ecology in Europe. *Preslia*, 2002, **74**, 373–393.
11. Austin, M. P., Community theory and competition in vegetation. In *Perspectives on Plant Competition* (eds Grace, J. B. and Tilman, D.), Academic Press, 1990, pp. 215–239.
12. Foster, B. L., Dickson, T. L., Murphy, C. A., Karel, I. S. and Smith, V. H., Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. *J. Ecol.*, 2004, **92**(3), 435–449.
13. Kowarik, I. On the role of Alien species in urban flora and vegetation. In *Urban Ecology* (eds Marzluff, J. *et al.*), Springer, USA, 2008, pp. 321–338.
14. Gupta, S., An ecological investigation on biomass production and allocation pattern of some weed flora at Bulandshahr. Ph D thesis, CCS University, Meerut, 2008.
15. Gaur, R. D., *Flora of the District Garhwal, North West Himalaya*, TransMedia, Srinagar (Garhwal), India, 1999.
16. Sharma, L. K., Floristic studies of district Bulandshahr and morphological studies of DasmodiumDesv. and Alysicarpur Neek. With special reference to fruit structure. Ph D thesis, Meerut University, Meerut, 1980.
17. Jackson, B. D., *Index Kewensis Plantarum Phanerogamarum*, Clarendon Press, Oxford, UK, 1895.
18. Khuroo, A., Reshi, Z., Malik, A., Weber, E., Rashid, I. and Dar, G., Alien flora of India: taxonomic composition, invasion status and biogeographic affiliations. *Biol. Invasions*, 2012, **14**(1), 99–113.
19. Khuroo, A. A., Dar, G. H., Khan, Z. S. and Malik, A. H., Exploring an inherent interface between taxonomy and biodiversity: Current problems and future challenges. *J. Nat. Conserv.*, 2007, **15**(4), 256–261.
20. Singh, K. P., Shukla, A. N. and Singh, J. S., State-level inventory of invasive alien plants, their source regions and use potential. *Curr. Sci.*, 2010, **99**(1), 107–114.
21. Pysek, P., Sadlo, J. and Mandak, B., Catalogue of alien plants of the Czech Republic. *Preslia*, 2002, **74**, 97–186.
22. Piper, C. S., *Soil and Plant Analysis*, Interscience Publications Inc., New York, USA, 1944.
23. Allen, S. E., Grismshaw, H. M. and Rowland, A. P., Chemical analysis. In *Methods in Plant Ecology* (eds Moore, P. D. and Chapman, S. B.), Blackwell Scientific Publication, 1986, pp. 285–344.
24. ter Braak, C. J. F. and Smilauer, P., *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5)*, Microcomputer Power (Ithaca, NY, USA), 2002.
25. Zhang, J. T., *Quantitative Ecology*, Science Press, Beijing, China, 2004.
26. Ahmad, A., *India: A General Geography*, NCERT Publications, New Delhi, India, 1999.
27. Marini, L., Gaston, K. J., Prosser, F. and Hulme, P. E., Contrasting response of native and alien plant species richness to environmental energy and human impact along alpine elevation gradients. *Global Ecol. Biogeogr.*, 2009, **18**(6), 652–661.
28. Ding, J., Mack, R. N., Lu, P., Ren, M. and Huang, H., China's booming economy is sparking and accelerating biological invasions. *BioScience*, 2008, **58**(4), 317–324.
29. Liu, J., Dong, M., Miao, S., Li, Z., Song, M. and Wang, R., Invasive alien plants in China: role of clonality and geographical origin. *Biol. Invasions*, 2006, **8**(7), 1461–1470.
30. Weber, E., Sun, S-G. and Li, B., Invasive alien plants in China: diversity and ecological insights. *Biol. Invasions*, 2008, **10**(8), 1411–1429.

31. Wu, S.-H., Sun, H.-T., Teng, Y.-C., Rejmánek, M., Chaw, S.-M., Yang, T. Y. and Hsieh, C.-F., Patterns of plant invasions in China: taxonomic, biogeographic, climatic approaches and anthropogenic effects. *Biol. Invasions*, 2010, **12**(7), 2179–2206.
32. Ng, S. C. and Corlett, R. T., The bad biodiversity: alien plant species in Hong Kong. *Biodivers. Sci*., 2002, **10**, 109–118.
33. Pyšek, P., Is there a taxonomic pattern to plant invasions? *Oikos*, 1998, **82**(2), 282–294.
34. Wu, S.-H., Hsieh, C.-F., Chaw, S.-M. and Rejmánek, M., Plant invasions in Taiwan: insights from the flora of casual and naturalized alien species. *Divers. Distrib.*, 2004, **10**(5-6), 349–362.
35. Zerbe, S., Choi, I.-K. and Kowarik, I., Characteristics and habitats of non-native plant species in the city of Chonju, Southern Korea. *Ecol. Res*., 2004, **19**(1), 91–98.
36. Gupta, S. and Narayan, R., Phenotypic plasticity of *Chenopodium murale* across contrasting habitat conditions in peri-urban areas in Indian dry tropics: Is it indicative of its invasiveness? *Plant Ecol.*, 2012, **213**(3), 493–503.
37. Rejmanek, M. and Richardson, D. M., What attributes make some plant species more invasive? *Ecology*, 1996, **77**(6), 1655–1661.
38. Huang, Q. *et al.*, Determinants of the geographical extent of invasive plants in China: effects of biogeographical origin, life cycle and time since introduction. *Biodivers. Conserv.*, 2010, **19**(5), 1251–1259.
39. McDougall, K. L., Alexander, J. M., Haider, S., Pauchard, A., Walsh, N. G. and Kueffer, C., Alien flora of mountains: global comparisons for the development of local preventive measures against plant invasions. *Divers. Distrib.*, 2011, **17**(1), 103–111.
40. Bloom, A. J., Chapin, F. S. and Mooney, H. A., Resource limitation in plants – an economic analogy. *Annu. Rev. Ecol. Syst.*, 1985, **16**(1), 363–392.
41. Gupta, S. and Narayan, R., Species diversity in four contrasting sites in a peri-urban area in Indian dry tropics. *Trop. Ecol.*, 2006, **47**, 229–241.
42. Gupta, S. and Narayan, R., Brick kiln industry in long-term impacts, biomass and diversity structure of plant communities. *Curr. Sci.*, 2010, **99**(1), 72–79.
43. Geng, Y.-P., Pan, X.-Y., Xu, C.-Y., Zhang, W.-J., Li, B. and Chen, J.-K., Plasticity and ontogenetic drift of biomass allocation in response to above- and below-ground resource availabilities in perennial herbs: a case study of *Alternanthera philoxeroides*. *Ecol. Res.*, 2007, **22**(2), 255–260.
44. von der Lippe, M. and Kowarik, I., Do cities export biodiversity? Traffic as dispersal vector across urban–rural gradients. *Divers. Distrib.*, 2008, **14**(1), 18–25.
45. Poorter, H. and Nagel, O. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. *Aust. J. Plant Physiol.*, 2000, **27**, 595–607.
46. Osone, Y. and Tateno, M., Applicability and limitations of optimal biomass allocation models: a test of two species from fertile and infertile habitats. *Ann. Bot.*, 2005, **95**(7), 1211–1220.

ACKNOWLEDGEMENTS. We thank the University Grants Commission, New Delhi for financial support. We also thank the anonymous reviewers for their valuable comments and suggestions that helped improve the manuscript.

Received 21 April 2015; revised accepted 27 February 2017

doi: 10.18520/cs/v113/i01/53-62