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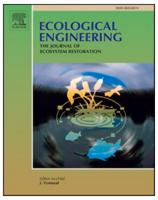

Plant adaptive strategy influences hydrologic services provisioning by stormwater bioretention

L. Krauss [a], M.A. Rippy [a,b,c,*]

[a] Occoquan Watershed Monitoring Laboratory, The Charles E. Via, Jr. Department of Civil and Environmental Engineering, Virginia Tech, 9408 Prince William Street, Manassas, VA, USA
[b] Center for Coastal Studies, Virginia Tech, 1068A Derring Hall (0420), Blacksburg, VA, USA
[c] Disaster Resilience and Risk Management (DRRM), 1068A Derring Hall, 405 Perry Street, Blacksburg, VA 17 24061, USA.

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ABSTRACT

Saturated hydraulic conductivity (Ksat) is a key performance variable in nature-based solutions for managing stormwater such as bioretention. Ksat is well understood from a soils perspective, but not an ecological one, despite growing recognition that plant traits and soil characteristics influence one-another and may co-regulate Ksat. There are myriad plant traits that potentially influence Ksat, which makes it difficult to know where attention should be focused to inform hydrologic design. We address this knowledge gap by 1) evaluating adaptive strategy theory as an overarching framework for characterizing plant effects on Ksat, assessing fifteen bioretention systems across three U.S. states and 2), exploring the implications of this theory for spatial and temporal patterns in plant effects on Ksat driven by regional variability in planting guidance and trajectories of plant succession. Our results illustrate that adaptive strategy significantly influences Ksat, with ruderal plants tending to decrease it and stress tolerant or competitive/stress tolerant plants increasing it. These relationships are indirect, reflecting the impact of adaptive strategy on root traits and soil organic matter, which influence Ksat directly. When these relationships are evaluated in the context of established planting guidance, we find that plants recommended in arid climates tend to increase Ksat relative to bare filter media whereas plants in humid climates do not. Small biases in planting preferences can dramatically change these outcomes. For instance, established vegetation in our bioretention sites was more competitive/stress tolerant than expected, significantly increasing Ksat. We also find that plant effects on Ksat are likely to vary in response to ruderal recruitment as bioretention systems age, reducing Ksat up to 15 %. Collectively, these results illustrate that plants play an important role in bioretention hydrology, and warrant consideration during hydrologic design. They also suggest that adaptive strategy theory is a promising design tool, providing useful insights into plant effects on Ksat, both geographically and over time.

1. Introduction

Capture and infiltration of urban runoff is a key service provided by many of today's nature-based solutions (NbS) for stormwater management, including small-scale, distributed systems such as bioretention swales, stormwater biofilters, and rain gardens that attempt to manage runoff at its source (Askarizadeh et al., 2015; Walsh et al., 2016). Infiltration is central to the capacity of such infrastructure to reduce urban flooding, an increasingly important service as climate change accelerates, extreme events become more common, and flood risk heightens (Green et al., 2021; Sanders and Grant, 2020; Schubert et al., 2017). It also exerts strong control over many other services, including water quality, public health, and aesthetic services, among others (Church, 2015; Muerdter et al., 2018; Sharma and Malaviya, 2021; Zawarus, 2022). The importance of infiltration for the performance of many NbS is evident in the prominence of infiltration-related design criteria in today's state and county design manuals (Missouri, 2012; MSM Wiki, 2023; ORSDM, 2014). Most manuals specify overall drainage time as a primary design regulation (e.g., the ponding zone must infiltrate within 24–96 h following a storm event) (Davis et al., 2009; DEQ, 2013; Ebrahimian et al., 2020; Zawarus, 2022). This makes soil hydraulic parameters like saturated hydraulic conductivity (Ksat) critical

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* Corresponding author at: Occoquan Watershed Monitoring Laboratory, The Charles E. Via, Jr. Department of Civil and Environmental Engineering, Virginia Tech, 9408 Prince William Street, Manassas, VA, USA.
E-mail address: mrippy@vt.edu (M.A. Rippy).

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for the design and performance of today's infiltrative NbS.

Ksat is a measure of a soil's ability to transmit water when fully saturated (i.e., it is the minimum, steady state value of the infiltration rate through saturated soils; Ebrahimian et al., 2020). In infiltrative NbS, Ksat is often manipulated through filter media properties, using USDA soil texture classes as a guide (Ebrahimian et al., 2020) (see Appendix A, Table 1a,b for a list of soil and other non-biologic design elements used to regulate Ksat in NbS). Although recommendations vary, A class subsoils are often specified (B or C if underdrains can be used), with media mixes ranging from sandy loam to sand (Clar et al., 2004; Davis et al., 2009; DEQ, 2013). Soil amendments such as organic matter and vermiculite are sometimes stipulated, as they have been shown to promote infiltration by reducing soil bulk density (DEQ, 2013; Le Coustumer et al., 2012; Skorobogatov et al., 2020; Técher and Berthier, 2023). Other considerations include sizing guidelines (e.g., catchment to infrastructure area ratios or drainage area caps; DEQ, 2013; Técher and Berthier, 2023), which are intended to 1) increase the amount of stormwater infiltrated by reducing the volume lost to overflow and 2) reduce compaction and clogging of filter media during large storms to preserve hydraulic conductivity (Ebrahimian et al., 2020; Técher and Berthier, 2023).

More recently, the role of vegetation in maintaining Ksat has also been considered (see Appendix A, Table 1c), with a handful of design manuals beginning to call attention to specific species or functional types that might have implications for Ksat in recommended plant lists (Alabama, 2007; MSM Wiki, 2023). Incorporating such information has been slow going, however, because it is not always clear how specific plants will impact Ksat or how best to use that information to inform design (Ebrahimian et al., 2020; Skorobogatov et al., 2020). Put another way, while there is increasing scientific consensus that plants play a meaningful role in regulating Ksat and are important to consider from an ecological design standpoint, the specific traits involved and the nature of their impact (i.e., increasing Ksat or decreasing it) are not always clear (Ebrahimian et al., 2020; Leung et al., 2015, 2018; Lu et al., 2020; Ng et al., 2020; Skorobogatov et al., 2020; Técher and Berthier, 2023; Yu et al., 2016). Complicating matters, the number of functional traits that have been implicated in regulating soil hydraulic properties is vast, including root diameter, specific root length, root length density, root mass density, root surface area density, and root volume density, among others (Appendix A, Table 1c, Ebrahimian et al., 2020; Lu et al., 2020; Skorobogatov et al., 2020; Técher and Berthier, 2023). This makes untangling their effects and identifying the best way of translating them into meaningful design criteria, difficult.

One path forward might be to leverage existing theoretical frameworks that organize plant traits into overarching functional types that might themselves be expected to influence soil hydraulic properties such as Ksat in NbS. This would allow us to account for functionally meaningful differences in plant composition on Ksat without necessitating species-level information on entire suites of individual functional traits. We hypothesize that plant adaptive strategy theory, originally proposed by Grime (1977), is an appropriate organizational framework for accomplishing this task. The theory recognizes a total of 19 plant adaptive strategies, with 3 principal endmembers (C – competitive, S – stress tolerant, and R – ruderal) that have fundamentally different modes of resource allocation and above/below ground plant traits that reflect them (Grime, 1977; Grime and Pierce, 2012; Hodgson et al., 1999).

Different adaptive strategies are delineated by stress (e.g., factors that harm plant physiology) and disturbance (e.g., factors that physically damage plant biomass), with stress fueling the resource conservation gradient (high stress environments favor resource conservative, stress-tolerant plants; low stress environments favor resource acquisitive, competitive or ruderal plants), and disturbance fueling the size gradient (disturbed environments favor plants with low biomass and short-lived plant structures such as weedy ruderals; stable environments favor the opposite) (Bergmann et al., 2020; Dunnett, 2015; Grime, 1977; Grime and Pierce, 2012; Hodgson et al., 1999). Responses to these gradients have trait-level implications, with each plant adaptive strategy being associated with its own characteristic functional trait suites (Appendix A, Table 1d). Initially these suites emphasized leaf, stem, and whole-of-plant traits, but root traits, including many that are linked to plant regulation of soil hydraulic properties in the literature, are increasingly featured (Bergmann et al., 2017, 2020; Freschet et al., 2021; Pierce et al., 2017; Reich, 2014). For instance, we now recognize that ruderal plants tend to have higher specific root lengths, lower root tissue densities and lower root diameters than plants with other adaptive strategies (Craine et al., 2001; Roumet et al., 2006). If fine root structures block soil pores and eliminate macropores as described by Lu et al. (2020), this could make ruderals more likely to clog NbS media than

Table 1
Bioretention characteristics.

Site	State	Age (years)	Area (m^2)	Depth (m)	Surface Area Ratio[1]	Current *(Initial)* media *S: Sand, LS: Loamy Sand*	SZ[2]	Dominant growth form (% understory cover, % canopy cover)	Planting Plan	Initial Diversity *P: polyculture, M: monoculture*
Catawba	NC	16	179	0.51	3.4	S *(S)*	N	forb (43%, 10%)	N	–
Duplin	NC	16	217	0.69	1.8	LS *(S)*	N	forb (84%, 32%)	Y[3]	P *(forbs & graminoids)*
Kensington A	MD	6	93	0.61	6.7	LS *(LS)*	N	tree (66%, 23%)	N	–
Kensington B	MD	6	33	–	–	LS *(LS)*	–	tree (15%, 63%)	N	–
Knightdale L	NC	10	188	0.66	9.4	S *(S)*	Y	forb (77%, 0%)	Y[4]	M *(graminoid)*
Knightdale S	NC	10	101	0.76	5.1	S *(S)*	Y	graminoid (80%, 0%)	Y[4]	M *(graminoid)*
Ridgeview	MD	6	35	0.41	2.6	LS *(S)*	N	tree (75%, 82%)	N	–
Science Museum	VA	7	89	0.76	4.8	LS *(S)*	N	tree (64%, 98%)	Y[5]	P (*trees, shrubs, forbs, graminoids*)
St. Agnes Lower	VA	7	27	–	–	S *(S)*	–	shrub (89%, 31%)	Y[5]	P (*trees, shrubs, forbs*)
St. Agnes Upper	VA	25	149	0.97	4.3	LS *(LS)*	N	tree (11%, 100%)	Y[5]	P (*trees, shrubs, graminoids*)
St. Andrews	MD	17	57	0.30	1.6	LS *(LS)*	Y	tree (5%, 100%)	N	–
UMD Creek	MA	17	26	0.91	2.3	LS *(LS)*	N	forb (87%, 25%)	N	–
UMD West	MA	6	22	0.46	0.4	LS *(LS)*	N	forb (97%, 0%)	N	–
UNC Mall	NC	18	90	1.02	14.9	S *(S)*	N	tree (44%, 100%)	N	–
US 258	NC	16	40	1.07	6.6	LS *(S)*	N	forb (98%, 0%)	Y[3]	M (*forb*)

[1] Surface Area Ratio: (NbS area/Catchment area) x 100.
[2] SZ: Submerged Zone.
[3] Planting plans from NCDOT.
[4] Planting plans from Luell et al. (2011).
[5] Planting plans from project personnel.

enhance infiltration. The inverse is also possible however, because ruderal plants allocate fewer resources to roots. This reduces their lifespan and could potentially increase hydraulic conductivity if preferential flow paths are created upon senescence (Cui et al., 2019). Differentiating between outcomes like these and determining which are more likely requires deepening our understanding of how adaptive strategy, root traits and Ksat interact in NbS, information that is critical for determining the ultimate value of plant adaptive strategy as an ecological design tool for these systems.

In addition to its microscale implications (e.g., links to specific root functional traits and their hydrologic impacts), plant adaptive strategy also has macroscale implications that may increase its value for ecological design. For instance, we already know the median (and range) of plant adaptive strategies in recommended plant lists for NbS across 8 of 11 major U.S. climate zones (Krauss and Rippy, 2022). This gives us a continent-scale snapshot of how today's planting guidance might impact plant strategies in NbS and, supposing that guidance is followed, a “sneak peek” at its potential hydrologic impacts in different climate zones. There is still a lot of work to do for this “sneak peek” to be possible; for instance, the extent to which adaptive strategy profiles from today's plant lists match those present in built infrastructure would need to be elucidated (Krauss and Rippy, 2022), as would the degree to which adaptive strategy, root trait, and Ksat relationships vary as a function of climate (Thompson et al., 2010). Even so, the capacity for scale-up is significant, and certainly one way adaptive strategy theory could provide added value for ecological design.

Another element of plant adaptive strategy theory with important implications for ecological design is succession (i.e., first order filtering of original vegetation, driven by system-specific gradients of stress and disturbance that cause plant communities in NbS to change over time in predictable ways; Grime and Pierce, 2012; Pierce et al., 2007). In green roofs, stress/disturbance profiles often favor ruderal or stress tolerant species over competitive ones, prompting loss in competitive plant species over time (Catalano et al., 2016; Dunnett, 2015; Lundholm et al., 2014; Thuring and Dunnett, 2019). Competitive exclusion, another well-recognized successional change, has the opposite effect, shifting plant communities towards competitive dominants and away from stress tolerant and ruderal species in low stress, low disturbance NbS (Levin and Mehring, 2015; Prévosto et al., 2011). Because succession involves adaptive strategy shifts, and adaptive strategy has the potential to influence soil hydrologic properties, it seems likely that adaptive strategy theory can be used as a theoretical basis for understanding how today's plant selection practices will impact the hydrologic performance of NbS in the long term. From a design standpoint this is extremely important. We don't want NbS to gradually lose functionality over time, but we also don't want to waste valuable resources attempting to combat succession (Dunnett, 2015; Krauss and Rippy, 2022). To the extent adaptive strategy theory helps address these challenges (to plan for succession rather than fight against it), it is likely to be an indispensable tool in our ecological design toolbox for NbS.

This study is organized around three principal objectives inspired by the knowledge gaps identified above: (1) to evaluate the utility of adaptive strategy theory as an overarching framework for understanding how plants influence soil hydraulic properties such as Ksat in NbS; (2) to provide a “sneak peek” at the implications of current planting guidance for Ksat in one of the largest U.S. climate zones (Cfa; humid subtropical), and generate testable hypotheses regarding plant effects on Ksat for 7 other climate zones; and (3) to characterize trajectories of plant succession in existing stormwater bioretention systems and explore their implication for long term hydrologic performance. In addressing these objectives, we hope to chart a possible path forward for ecologically-informed hydrologic design. Our results suggest that planning for plant effects is not out of reach, and that bringing plant adaptive strategy into the overall design process could provide added value, particularly when designing for long term hydrologic performance.

2. Methods

2.1. Field site description

Fifteen stormwater bioretention systems were selected for this study, following a prior design described in Waller et al. (2018). The systems span three states (Maryland, Virginia, and North Carolina), all within the humid subtropical Koppen-Geiger climate zone, the second largest climate zone in the conterminous United States (Cfa; mean annual rainfall: 1463 mm, no significant difference in precipitation between seasons; Kottek et al., 2006). Initial design characteristics for each bioretention system are outlined in Table 1. Systems ranged in size from roughly 22 m^2 at UMD West to 217 m^2 at Duplin and had surface area to catchment area ratios ranging from 0.37 (UMD West) to 14.9 (UNC Mall). Filter media was loamy sand or sand, and, at the time of sampling, system ages ranged between 6 and 25 years. Planting plans were variable, with some systems planted as monocultures (e.g., the two Knightdale bioretention cells), and others planted as polycultures with diverse assemblages of grasses, forbs, and trees (e.g., the Science Museum and St. Agnes Upper).

2.2. Sample collection and processing

2.2.1. Vegetation cover

Vegetation surveys were conducted at each bioretention system using the point intercept transect method, with plants identified to the species level, facilitating species-specific cover estimates (Caratti, 2006; Kuo et al., 2022; Mueller-Dombois and Ellenberg, 1974). To best represent vegetation communities, sampling transects spanned both basin bottom and side slope regions of each bioretention cell, stopping at the upper edge of the ponding zone. Transects (and points along them) were spaced $\leq$ 2 m apart (i.e., they were never wider than the widest plant; Caratti, 2006). Approximately 100 points were sampled per site, allowing plant cover (understory and canopy) to be assessed at a minimum of 1% resolution. Species specific cover (cover_{sp}) was estimated using the following equation: $\text{cover}_{sp} = \frac{p_{sp}}{p_t} \times 100$, where p_{sp} is the number of points where a species was detected, and p_t is the total number of sampled points. Any species with >10% cover (understory or canopy) was considered a dominant plant species. The remainder of our sampling program was structured around these species, taking advantage of their tendency to co-occur in large, monospecific clumps that make it easier to link above-ground traits and plant adaptive strategy to root traits, soil characteristics, and Ksat, and evaluate relationships between them at a species-specific level (Craine et al., 2001; Fort et al., 2013; Virahsawmy et al., 2014). The methods we employed for above and below-ground vegetation sampling (e.g., for adaptive strategy and root traits), filter media sampling, and saturated hydraulic conductivity measurements are described below.

2.2.2. Adaptive strategy classification

At each bioretention cell leaf tissue was collected from ten representative specimens of each dominant plant species (two mature leaves per specimen; 20 leaves per species) for use in adaptive strategy classification. Leaf clippings were stored in a cooler and transported to the lab for analysis. All analyses were performed accordance with standard methods from (Cornelissen et al., 2003). Briefly, leaves were refrigerated in a moist paper towel for 24 h to hydrate and then blotted dry and weighted to estimate leaf fresh weight. Leaf area (single sided) was measured using a Li—3100C leaf area meter (LiCor Incorporated, NE). Afterwards, all leaves were placed in a drying oven at 60 °C for 72 h and weighed to estimate leaf dry weight. Leaf dry matter content (LDMC) was calculated as the ratio of leaf dry weight to leaf fresh weight, and specific leaf area (SLA) was calculated as the ratio of leaf area to leaf dry weight. The adaptive strategy of each dominant plant species was estimated from measured leaf area, SLA, and LDMC using a series of globally calibrated equations developed by Pierce et al. (2017) (Appendix A, Table 2).

2.2.3. Root trait analysis

Soil cores were collected adjacent to two of the ten plant specimens where leaf tissue was collected, for each dominant plant species (AMS split core sampler, AMS Inc., ID; 5 cm diameter, 30.5 cm length). Additional cores (2 per site) were collected at bare ground locations as "unplanted" controls. Cores associated with individual plant species were taken from specimens within monospecific clusters that were at least 0.3 m away from other plant species. Sampling was conducted as close to the mainstem as possible. Soil cores were preserved in a solution of 70% ethanol, 25% glycerol and stored in a dry, dark, place until they could be processed.

Soil cores were processed by manually separating roots from soil using a dissecting microscope under 10× magnification. Roots were rinsed with DI water to remove residual soil, dyed using 1.4% methylene blue dye for improved visualization, and then scanned in a water-filled Perspex tray using a Regent STD4800 scanner (Payne et al., 2018). Scanned images were analyzed using WinRHIZO Pro software (version 2020b, Regent Instruments, Canada Inc.) to determine total root length, total root volume, average root diameter (RD), and fine root length (FRL; length of roots <0.25 mm in diameter). Following image analysis, samples were dried for at least 48 h in a 60 °C drying oven and then weighed to estimate root dry weight (Winfrey et al., 2018). Specific root length (SLR) was calculated as the ratio of total root length and root dry weight, root tissue density (RTD) was calculated as the ratio of root dry weight to root volume, and root length density (RLD) was calculated as the ratio of total root length to soil core volume.

2.2.4. Filter media characterization

Two filter media characteristics were evaluated in this study (organic matter content and median particle size; D50), both of which have been shown to influence infiltration (Sun et al., 2016; Zhao et al., 2013). Soil characteristics were measured using composite soil samples, approximately 10 cores per site (2.54 cm in diameter, 30.5 cm long), totaling 200 g of soil per system. All cores were collected from the basin bottom region where the majority of infiltration occurs. Samples were air dried for 1–2 weeks (Robertson, 1999) and ground to break up large aggregates using a Gilson soil grinder (SA-45, Gilson Company Inc., OH). Median soil diameter was calculated in accordance with NIST particle size characterization guidelines using six nested sieves (#8, #16, #30, #50, #100, #200) and a Gilson SS-3 vibratory sieve shaker (Gilson Company Inc., OH), run for 10 min per sample at a frequency of 60 taps per minute (Jillavenkatesa et al., 2001). Soil organic matter content was estimated as described in ASTM D2974 (ASTM, 2020). Briefly, 50 g of soil were dried for 24 h in a 105 °C oven to estimate soil dry weight and then combusted in a muffle furnace for 4 h at 360 °C to estimate ash dry weight. The difference (i.e., ash-free dry weight) became our estimate of soil organic matter content.

2.2.5. Saturated hydraulic conductivity

In each bioretention system saturated hydraulic conductivity was measured at three bare ground locations and three planted locations per dominant plant species. This works out to between 9 and 15 Ksat measurements per site. Two-thirds of these measurements were coincident with soil core collection for root trait analysis - Ksat was always measured first to preserve soil hydraulic properties. Ksat measurements were made using a Modified Phillip Dunne infiltrometer, a form of falling head infiltrometer, in accordance with standard methods (ASTM D8152; ASTM, 2022). All measurements were made during summer months so that the contribution of temperature to Ksat variability would be minimal. Measurements were temperature corrected to 31.8 °C (the average temperature across all sites during sample collection; HOBO MX2301A Temperature/RH data logger, MA, USA), as described in Ebrahimian et al. (2020).

2.3. Statistical methods

2.3.1. Ordination and factor projection – Linking plant adaptive strategy to root traits

Principal component analysis (PCA) and factor projection were used to determine if above-ground leaf traits used to estimate plant adaptive strategy (leaf area, SLA, LDMC; Pierce et al., 2017) were associated with root traits suspected to influence soil hydraulic properties in bioretention systems (e.g., RTD, SRL, RLD, RD, FRL – Appendix A, Table 1). Both analyses were conducted using R software (packages FactoMineR and factoextra, R version 4.1.2; Lê et al., 2008). PCA was performed on leaf traits first to separate out bioretention plant species by adaptive strategy. Leaf traits were transformed prior to analysis as in Pierce et al. (2017). A resampling-based stopping rule was used to identify principal component modes that explained more variability than expected due to chance – only these modes were retained and interpreted (Peres-Neto et al., 2005; Rippy et al., 2017). Following PCA, environmental factor projection was used to project root traits onto the ordinal space for leaf traits that characterize plant adaptive strategy (Davis, 2002). Root traits that load significantly on this ordinal plane can be considered meaningfully associated with plant adaptive strategy ($p < 0.05$ level). Significance was assessed using bootstrapped Pearson's correlations, where the variables being correlated were 1) raw root traits (prior to being transformed into PC space) and 2) predicted root traits (i.e., the dot product of the first two PC scores and the projection matrix used to transform raw root traits into PC space). Predicted traits only approximate raw traits if the relationship between those traits and the patterns in plant adaptive strategy captured by the original PCA is strong (Rippy et al., 2021).

2.3.2. Nonparametric bootstrapping and regression - characterizing plant effects on Ksat

Nonparametric bootstrapping (Matlab v2022a, Mathworks, MA) was used to determine if average Ksat varied significantly by plant adaptive strategy and if different plant strategies increased or decreased Ksat relative to bare filter media. Briefly, Ksat measurements were sorted into eight groups (one for bare ground measurements and 7 for measurements made adjacent to different plant strategies; C, S, R, CS, CR, SR, CSR). Ten-thousand bootstrapped realizations of average Ksat were generated for each group. Bias corrected and accelerated confidence intervals were estimated for each average and used to identify significant differences in Ksat across groups (95% CI's, corrected for multiple comparisons using the Benjamini-Hochberg false discovery rate; Benjamini and Hochberg, 1995).

Regression was used to evaluate the magnitude and significance of relationships between individual root traits and Ksat. Regressions were fit to log-transformed data using R (package stats, R Software). Significance was determined at a $p < 0.05$ level (F-test; Hahs-Vaughn and Lomax, 2020). 95% bootstrapped confidence bounds were estimated for each significant regression using residual (fixed-x) resampling (Davison and Hinkley, 1997).

2.3.3. Path analysis - considering plant effects in context

Path analysis was used to determine how plant adaptive strategy, root traits, and filter media composition interact to regulate Ksat as well as to benchmark plant effects on Ksat with filter media effects, which are more often the focus engineering design (package lavaan, R Software; Rosseel, 2012). In our initial path model, all possible direct and indirect paths were simulated (i.e., all plant and soil variables were presumed to impact one-another as well as Ksat). The following variables were included: median soil diameter (D50), soil organic matter content (SOM), plant adaptive strategy (C, S, R, CS, CR, SR, CSR), three root traits (RTD, SRL, RD), and a composite variable representing root length (the first principal component of FRL and RLD, two variables that were highly colinear (Pearson's correlation of 0.93) and needed to be evaluated collectively to avoid inflating model error; Maruyama, 1998).

Our proposed path model was evaluated for significance and refined using backwards elimination (Rippy et al., 2022). In this approach paths that are not significant at a $p < 0.05$ level are sequentially removed, starting with the least significant and continuing either until all remaining paths are significant or additional path removal increases the Bayesian Information Criterion, indicating that further increases in model parsimony are not worth associated decreases in overall variance explained (Beaujean, 2014). The following global metrics were used to assess final model fits: the Sattora-Bentler χ^2 test, the comparative fit index (CFI) and the standardized root mean squared residual (SRMR; Beaujean, 2014). Post-hoc power analysis was used to determine the statistical power of the final fitted model, given the number of samples supporting each relationship (package simsem, R Software). Significant relationships ($p < 0.05$ level) with moderate to low statistical power (i.e., < 0.7) should be interpreted with caution - a larger study is required to confirm or refute them (see Rippy et al., 2022).

A likelihood ratio test was used to determine the relative importance of plant and filter media effects in the final fitted model (package lavaan, R Software). Briefly, the test compared the fit of a restricted model (i.e., with all plant and filter media effects assigned the same standardized coefficient) to the final fitted model. Plant and filter media effects should be considered comparable in magnitude if the two models do not significantly differ (Chi-squared difference; $p < 0.05$ level). 95% confidence intervals were also generated about the standardized coefficients for all direct and total effects in the final fitted model, allowing the impact of each plant and soil variable on Ksat to be directly compared.

2.3.4. *Bootstrap predictions of Ksat by climate zone – Implications of current planting guidance*

Krauss and Rippy (2022) report confidence clouds (i.e., 3-dimensional confidence bounds) about the median adaptive strategy of recommended bioretention plants from each major Koppen-Geiger climate zone. We used these clouds to estimate how current plant guidance might affect Ksat in different US climate zones. Briefly, the fraction of confidence cloud area occupying each adaptive strategy region of C-S-R space was used to estimate the probability that the median adaptive strategy in each climate zone was C, S, CS, SR, CR, or CSR. These probabilities were used as weights in a weighted nonparametric bootstrap of our empirical Ksat measurements (Davison and Hinkley, 1997). In this bootstrapping procedure, planted Ksat measurements (drawn from different adaptive strategy pools based on their probability of occurrence in a given climate zone) were paired with bare ground Ksat measurements, and the ratio of the two (planted/bare) was used to estimate average plant effect. This process was repeated 10,000 times for each climate zone, allowing zone-specific distributions of average plant effect to be estimated.

An additional plant effect calculation was made for climate zone Cfa. Cfa is the only climate zone where it was possible to compare estimated plant effects based on current planting guidance to measured plant effects in the field (i.e., from this study). Measured plant effects were evaluated using the same procedure described above, with adaptive strategy weights estimated from empirical data rather than confidence clouds from the literature. This makes the final weighted bootstrap a reflection of observed planting practices instead of recommended ones.

2.3.5. *Bootstrap predictions of Ksat over time – The impact of plant succession*

At each site where original planting plans were available, plants were separated into original and volunteer species, the median adaptive strategy of each group was estimated, and the difference between the two was used to characterize site-specific plant trajectories. Sites with similar trajectories (for instance, stress tolerant to competitive) were pooled, forming trajectory groups, and evaluated collectively to increase statistical power. The following procedure was used. Planted Ksat measurements were divided by bare ground measurements to estimate relative plant effects at each site within a trajectory group. Next, a weighted nonparametric bootstrap was conducted at different levels of volunteer plant cover (0%, 5%, 10%, 20%, 40%, 60%, 80%, 100%) to determine the impact of volunteers on overall plant effects (Davison and Hinkley, 1997). Because each site had different original plantings, and therefore different plant effects at 0% volunteer cover, all results were expressed as percent change in plant effect relative to original site conditions:

$$\%\text{change PE} = 100 \times \frac{PE_v(x) - PE_o}{PE_o},$$

where %change PE is the percent change in plant effect, PE_v is the plant effect at $x > 0\%$ volunteer plant cover and PE_o is the original plant effect at 0% volunteer cover.

3. Results

3.1. *Associations between leaf and root traits*

PCA revealed two significant modes ($p < 0.01$ level) that explained 86% of the variance in leaf traits across bioretention systems (Fig. 1). PC

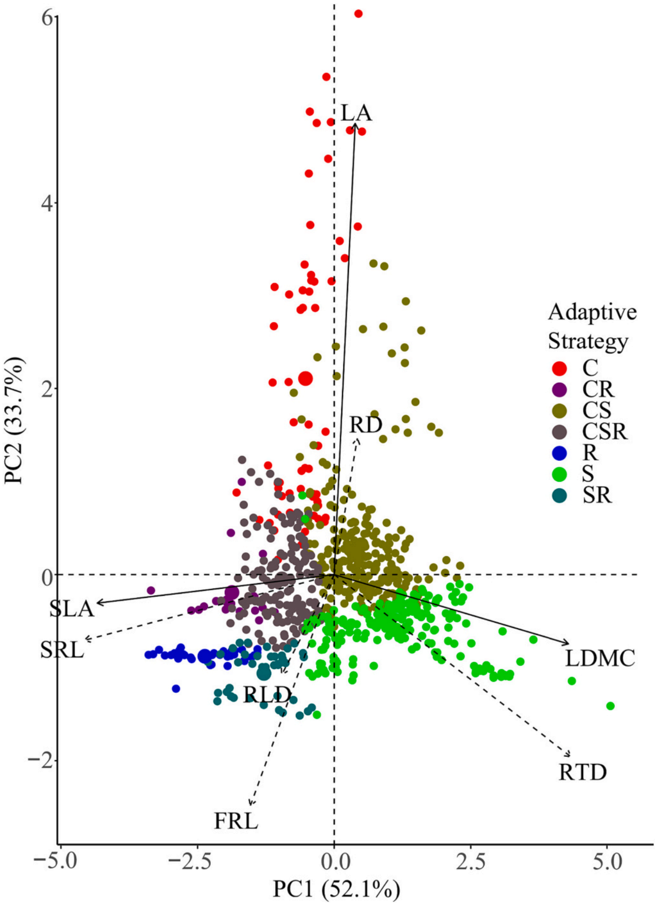

Fig. 1. Biplot illustrating dominant patterns in leaf traits from bioretention plants that are used to define plant adaptive strategy. The first principal pattern (PC1) is on the *x*-axis: positive PC1 indicates stress tolerance, negative PC1 indicates ruderalness. The second principal pattern (PC2) is on the *y*-axis: positive PC2 indicates competitiveness. Observations (points) are colored by plant adaptive strategy (red: C-type, purple: CR-type, tan: CS-type, grey: CSR-type, blue: R-type, green: S-type, teal: SR-type). Dashed lines represent root traits that have been projected onto the ordinal space for leaf traits. The strike of each root trait vector indicates the leaf traits and associated plant adaptive strategies each root trait is most correlated with. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mode 1 distinguished plants that are more stress tolerant (high LDMC, low SLA; positive PC1) from plants that are more ruderal (low LDMC, high SLA; negative PC1), whereas PC mode 2 distinguished plants based on their competitiveness (more - high leaf area, positive PC2; less - low leaf area, negative PC2). Factor projection (black dashed lines, Fig. 1) illustrate that root traits were significantly correlated with leaf traits characterizing different plant adaptive strategies. Root diameter (FRL, RLD) was positively (negatively) correlated with leaf area (competitiveness), SRL was positively correlated with SLA (ruderalness), and RTD was positively correlated with LDMC (stress tolerance).

This analysis was invariant to the order of operations performed (i.e., when a root trait PCA was performed followed by factor projection with leaf traits, the resultant ordination was nearly identical; see Appendix A, Fig. S1). This suggests not only that root and leaf traits are associated, but that their dominant patterns are (i.e., there appears to be strong mirroring between above and below ground plant traits in bioretention systems, such that differences in plant adaptive strategy are evident across both).

3.2. *Adaptive strategy and root trait influence on Ksat*

Measured Ksat values ranged from 38 to 4044 mm/h, with a geometric mean of 638 mm/h. No Ksat measurements were below the lower limits recommended for Ksat in stormwater bioretention (12.5–25.4 mm/h, leftmost dashed line, Fig. 2a; (CASQA, 2003; Hunt and Lord, 2006; MSM Wiki, 2023). Sixty-two percent, however, were above recommended upper limits for Ksat (300–500 mm/h, rightmost dashed line, Fig. 2a; FAWB, 2009).

Plant adaptive strategy and individual root traits both significantly influenced Ksat (Fig. 2). Ksat measurements made adjacent to plants with CS-type, S-type, and SR-type strategies (yellow, green, and teal distributions; Fig. 2a) were significantly higher than measurements made adjacent to plants with R- type strategies (blue distribution; Fig. 2a). CS-type plants were associated with Ksat values that exceeded bare filter media more often than other plant strategies (marginally significant at a $p < 0.1$ level; note the right shift of the yellow distribution for CS-type plants relative to the solid black 95% confidence bounds for bare ground filter media in Fig. 2a). S-type, C-type, SR-type, and CSR-type plant strategies were associated with more intermediate Ksat values, generally consistent with bare ground (green, red, teal, and grey distributions, respectively; Fig. 2a). R-type and CR-type plants were associated with lower Ksat values, with the geomean for R-type plants falling significantly below bare ground filter media. When bioretention systems with different media types (i.e., sand vs loamy sand) are evaluated separately, similar adaptive strategy patterns are observed; CS-type plants are associated with the highest Ksat values and R-type plants are associated with the lowest Ksat values across both media types (note that CS and S-type plants increase Ksat more in sandy filter media and R-type plants decrease Ksat more in loamy sand filter media; Appendix A, Fig. S2).

Root diameter and RTD were significantly and positively correlated with Ksat, whereas SRL was significantly and negatively correlated with Ksat ($p < 0.05$ level; Fig. 2b,c,f). The strongest of these relationships was with SRL (Pearson's correlation: −0.57), followed by RD (Pearson's correlation: 0.38), and RTD (Pearson's correlation: 0.31). Root length variables (FRL and RLD) exhibited no significant relationship with Ksat (Fig. 2d,e).

3.3. *Relative influence of root and filter media characteristics on Ksat*

Global fit metrics for our final path model were strong, suggesting that our conceptual framework for modeling Ksat using plant adaptive

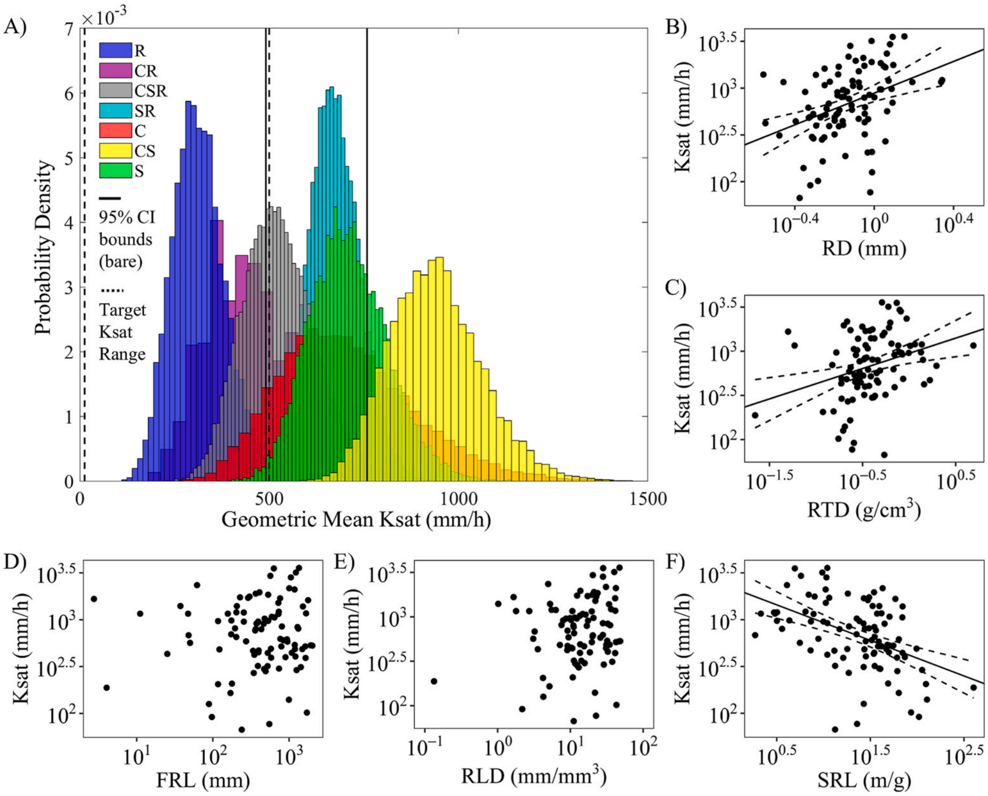

Fig. 2. (A) Bootstrapped distributions of mean saturated hydraulic conductivity (Ksat) for each plant adaptive strategy (colored probability distributions) and bare ground (solid black 95% confidence bounds). Dashed lines indicate target Ksat ranges from the literature. (B—F) Linear regressions of Ksat and root traits (B: root diameter, C: root tissue density, D: fine root length, E: root length density, and F: specific root length). Best-fit lines (solid) and 95% confidence bounds (dashed) are displayed for all significant regressions ($p < 0.05$ level).

strategy, root traits, and filter media characteristics was reasonable (χ^2 p-value: 0.92; comparative fit index: 1.0; standardized root mean square residual: 0.04). However, the model explained only 34% of observed variance in Ksat, illustrating that although plant adaptive strategy, root traits, and filter media characteristics significantly influence saturated hydraulic conductivity, they have limited predictive power when considered on their own.

Not all hypothesized relationships in the original path model were found to be significant. Relationships that were and exhibited high (moderate to low) statistical power are shown using solid black (grey) lines in Fig, 3a. Plant adaptive strategy was found to influence saturated hydraulic conductivity indirectly through root traits and soil organic matter content. C-type plants increased SOM content, had shorter root systems (low C.RL) and low RTD; CS-type plants had low SRL and high RTD; SR-type plants had low RD and high RTD; S-type plants decreased SOM content and had low SRL, high RTD, and low RD; CR-type plants had low C.RL; R-type plants had high SRL and low RD; and CSR-type plants had low RD.

Root traits (SRL, RD, C.RL) and filter media characteristics (D50, SOM) primarily influenced Ksat directly, with D50 also exhibiting indirect effects on Ksat through soil organic matter content and specific root length (Fig. 3a). Of these direct relationships, three had high statistical power: SRL decreases Ksat, C.RL increases Ksat, and D50 increases Ksat. Although these relationships differed in their absolute effect magnitudes (compare standardized coefficients, Fig. 3a), these differences were not significant at a $p < 0.05$ level (i.e., the direct effects of root and filter media characteristics evaluated here can be considered statistically comparable; grey bars, Fig. 3b). Because plant adaptive strategy only influenced Ksat indirectly, its total effects on Ksat were smaller than root traits or filter media characteristics (compare blue bars across all variable types, Fig. 3b). This said, the total effects of S and CS-type plants on Ksat were statistically comparable to direct and total effects for D50, SOM, C.RL, and RD ($p < 0.05$ level, Fig. 3b). The same is true for R-type plants and SRL. Other adaptive strategies had more intermediate and marginal effects on Ksat, consistent with Fig. 2a.

3.4. Predicted Ksat distributions by climate zone

In climate zone CFA the median adaptive strategy of recommended plants in bioretention plant lists is CSR (see large black circle and 95% confidence cloud, Fig. 4). The median adaptive strategy observed in the field, however, exhibited significantly more anti-ruderal bias, classifying cleanly as CS (white circle and 95% confidence cloud, Fig. 4). Looking at each bioretention system individually, seven contained plants with a median strategy of CS, four contained plants with a median strategy of S, two contained plants with a median strategy of CSR (or CSR/CR), and one contained plants with a median strategy of C. No systems contained predominantly R or SR type species.

Because CS-type plants and R-type plants represent Ksat endmembers (i.e., they are associated with the fastest and slowest, Ksat values, respectively; Fig. 2a), the above-noted biasing towards CS-type species and away from ruderal ones in climate zone CFA significantly influences plant effects on Ksat in that zone (see Fig. 5e). This is evident in the positive skew of median plant effects from field systems relative to predictions based on current planting recommendations (compare checkered and solid green distributions in Fig. 5e; effects >1 indicate that plants increase Ksat relative to bare ground and effects <1 indicate that plants decrease Ksat relative to bare ground). These differences

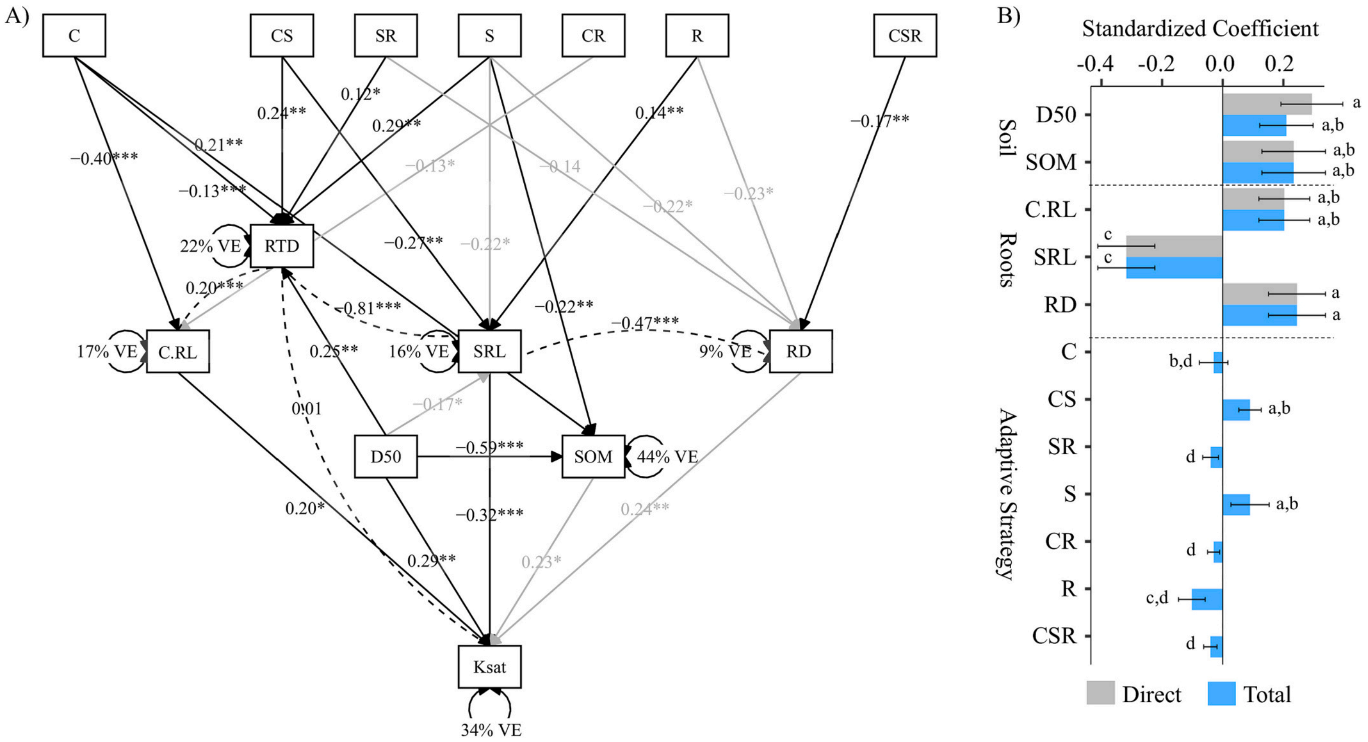

Fig. 3. (A) Path diagram illustrating the relationships between plant adaptive strategy, root traits, soil characteristics and saturated hydraulic conductivity. Stars indicate the level of significance of each modeled relationship (no star: $p < 0.1$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). Solid black lines represent significant relationships with high statistical power (power > 0.7). Grey lines represent relationships that are significant or marginally significant ($p < 0.1$), and have low to moderate statistical power (power < 0.7). Dashed lines represent significant model covariances. (B) Standardized path coefficients illustrating the magnitude of direct (grey) and total (direct plus indirect, blue) effects of soil characteristics, root traits, or plant adaptive strategy on Ksat. Error bars represent the standard error about each effect. Letter designations indicate effects that are significantly different with 95% confidence. Abbreviations: C, S, R, CS, SR, CR, CSR – Grime's plant adaptive strategies; RTD - root tissue density, C.RL - the first principal component of fine root length and root length density; SRL - specific root length; RD - root diameter; D50 - median particle diameter; SOM - soil organic matter content; and Ksat - saturated hydraulic conductivity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

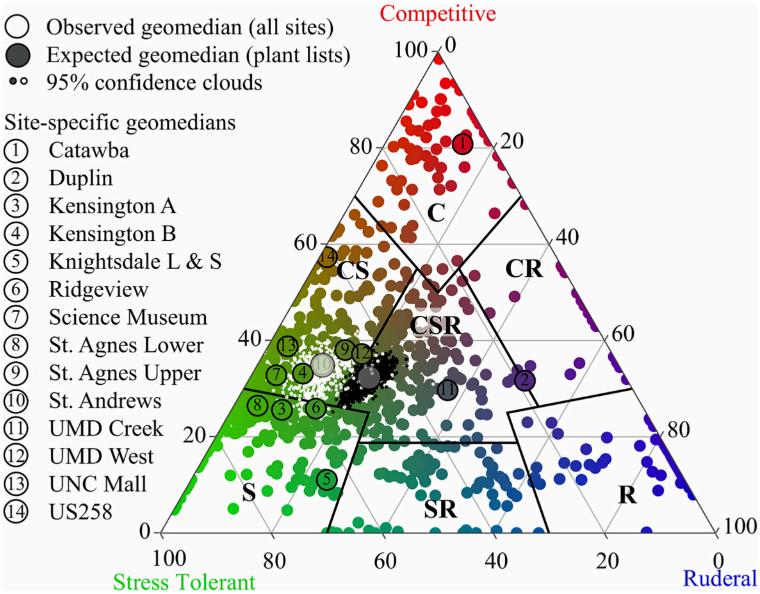

Fig. 4. Plant adaptive strategies in established bioretention cells from climate zone CFA. Colored symbols are individual plants. Numbered circles indicate the geomedian strategy for each bioretention cell. Large and small white circles indicate the observed geomedian strategy and 95% confidence cloud across all evaluated sites. Large and small black circles indicate the expected geomedian strategy and 95% confidence cloud based on planting recommendations for bioretention from climate zone CFA (taken from Krauss and Rippy, 2022).

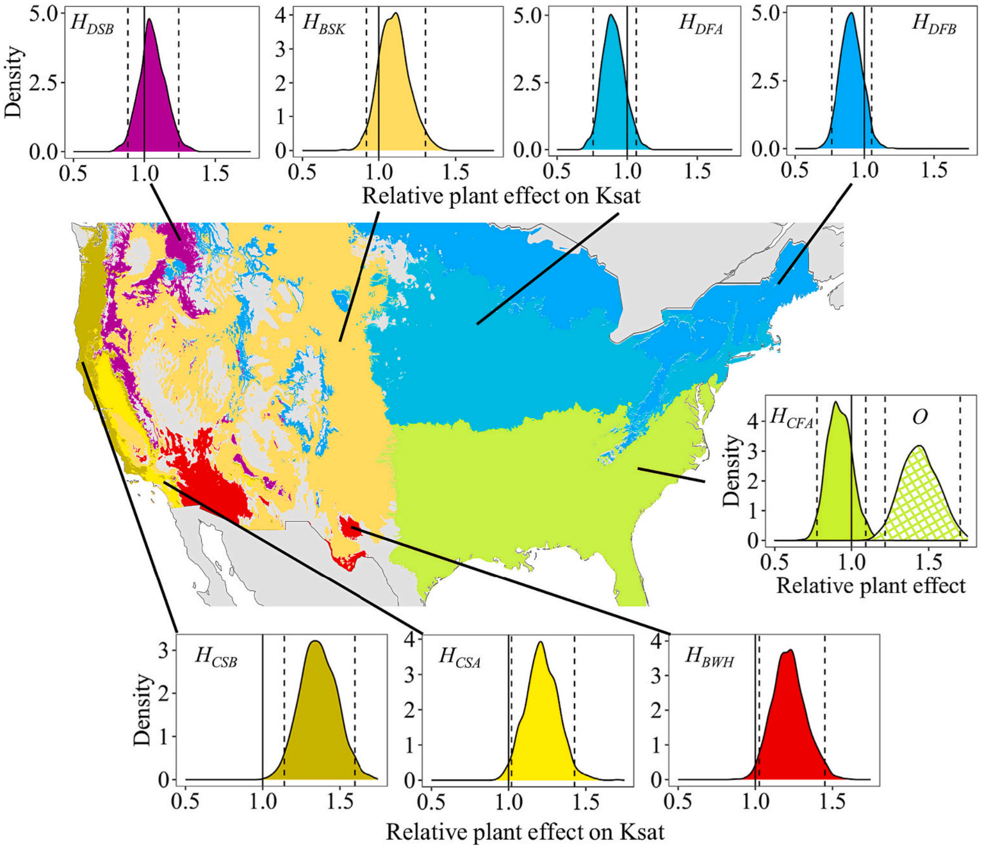

Fig. 5. Major climate zones of the continental US with hypothesized Ksat distributions estimated using the median adaptive strategy of recommended plant species and the observed relationships between plant adaptive strategy and Ksat reported in Fig. 2a. Distributions are shown as probability density functions, with 95% confidence bounds as vertical dashed lines. Colors represent climate zone; Dfb: purple, Bsk: orange, Dfa: light blue, Dfb: blue, Csb: tan, Csa: yellow, Bwh: red, Cfa: green. Both hypothesized and measured Ksat distributions are shown for CFA (left and right, pdfs, respectively). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

illustrate how dramatically relatively small changes in planting practices along the R to CS adaptive strategy continuum can influence plant effects on Ksat in bioretention systems.

If we presume that present planting recommendations are followed in the other 7 major US climate zones (Krauss and Rippy, 2022), we'd expect to see regions with more arid and Mediterranean climates, where planting guidelines bias towards S and CS-type plants, exhibit positive plant effects (i.e., plants increasing Ksat; BWH, CSA, CSB, and to a lesser extent BSK, see red, yellow, tan, and orange distributions, Fig. 5). Conversely, we'd expect to see regions that are humid-continental, where planting guidelines favor CSR or C-type plants, exhibit more neutral to slightly negative plant effects (i.e., plants maintain Ksat comparable to bare ground or slightly reduce it; DFA, DFB, DSB, blue and purple distributions, Fig. 5).

3.5. Predicted changes in Ksat over time due to plant community transitions

Seven of the 15 bioretention sites evaluated in this study had planting plans available, allowing original and volunteer plant species to be distinguished. Four of these sites exhibited a shift towards more ruderal plant species over time (Duplin, Science Museum, Knightsdale S and L), two exhibited a shift towards more competitive plant species (St. Agnes Lower, US258) and one exhibited no significant change in plant adaptive strategy (St. Agnes Upper) (Fig. 6a).

Consistent with the Ksat distributions in Fig. 2a, no change in plant effects on Ksat were evident in simulations where the proportion of competitive volunteers increased relative to original plantings (Fig. 6b). In simulations where the proportion of ruderal volunteers increased, however, plant effects on Ksat became larger and more negative (i.e., ruderal volunteers decreased Ksat relative to original plant species and this effect was greatest when the proportion of ruderal plants was largest; see Fig. 6c). The median percent change in plant effects on Ksat ranged between 2% (at 5% ruderal cover) and 15% (at 100% ruderal cover). These changes were not significant at a $p < 0.05$ level, which is likely a consequence of the stabilizing effect of other plant species on Ksat at different levels of volunteer species. Even when volunteer cover is 100% these simulations presume that original plant species are present and co-occupy space, forming different vertical strata (i.e., 100% cover of one plant species does not imply 0% cover of others).

4. Discussion

The principal goal of this study was to evaluate the utility of adaptive strategy theory as an overarching framework for understanding how plants influence soil hydraulic properties such as Ksat in stormwater bioretention. Our results suggest 1) that there is strong coupling between the above-ground leaf traits that characterize plant adaptive strategy and root traits that regulate infiltration (see Fig. 1), and 2) that both plant adaptive strategy and root functional traits significantly influence Ksat in established bioretention systems (see Fig. 2), with adaptive strategy influencing Ksat indirectly through root traits and soil characteristics like SOM, rather than directly (Fig. 3a). Although the indirect nature of the relationship between plant adaptive strategy and Ksat could be cause for concern, the strength of that relationship (see Fig. 2a) and the relative ease with which adaptive strategy is measured and could be incorporated into planting guidance, suggest that adaptive strategy theory could be a useful framework for identifying plants that improve hydrologic services in stormwater bioretention. Given the magnitude and significance of their impacts on Ksat relative to bare ground, CS, R, and to a lesser extent S-type plants appear to have the most potential for influencing hydrologic services in stormwater bioretention through targeted ecological design (see standardized path coefficients in Fig. 3b and Ksat distributions in Fig. 2a).

The coupling we observed between leaf and root traits (Fig. 1) is consistent with the fast-slow plant economic spectrum recognized by Reich (2014). This framework predicts that above and below ground plant traits are coordinated and should show similar adaptive patterns along resource gradients (Díaz et al., 2016; Reich, 2014; Shen et al., 2019). Strong coordination across plant organs has been observed in

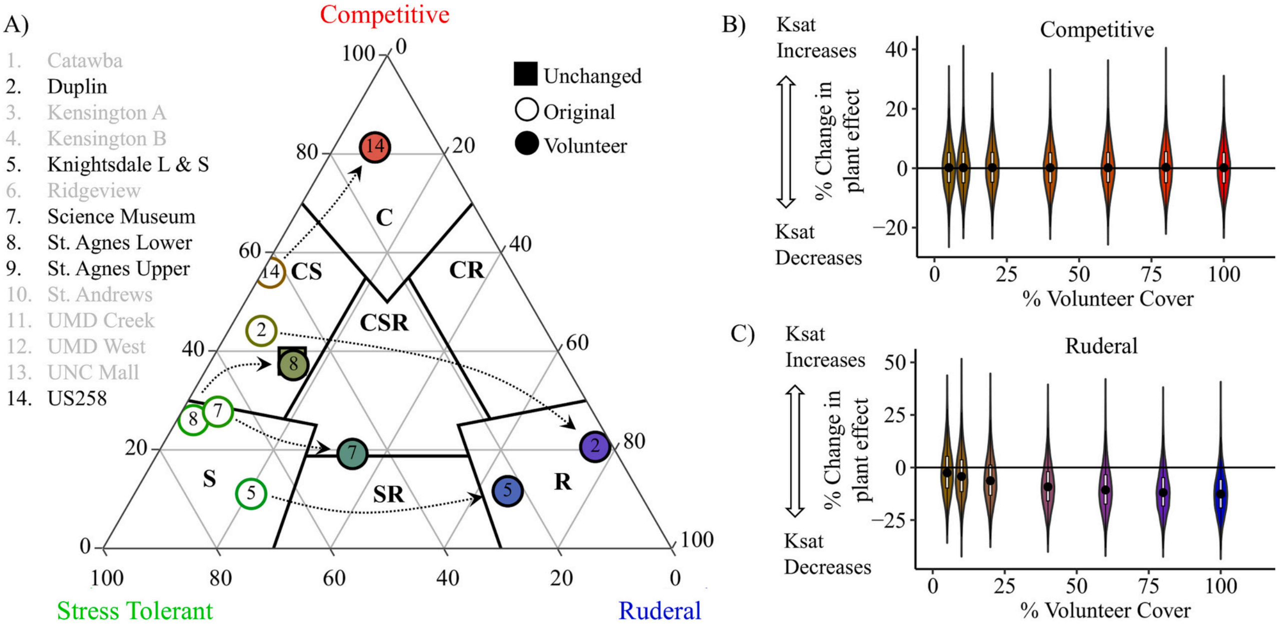

Fig. 6. (A) Trajectories in plant adaptive strategy at seven bioretention systems where planting plans were available (black text). Trajectories begin at the geomedian strategy of original plantings (open circles) and end at the geomedian strategy of volunteer recruits (closed circles). Squares indicate instances where the geomedian strategy did not change. (B) The percent change in the effect of plants on Ksat relative to bare ground in response to increasing cover of competitive plants. Two sites where competitive plants recruited and became prevalent were used as the basis for this analysis (US258, and St. Agnes Lower). (C) The percent change in the effect of plants on Ksat relative to bare ground in response to increasing ruderal plant cover. Four sites where original plantings were CS/S and self-recruitment of ruderal volunteers took place were used as the basis for this analysis (Duplin, Science Museum, Knightdale Small, and Knightdale Large). In both (B) and (C), positive (negative) changes in plant effect indicate that ruderal plants increase (decrease) Ksat relative to bare ground.

other studies, including several of the relationships identified here, suggesting they may be relatively common (e.g., the association between SRL and SLA, Freschet et al., 2015; Reich, 2014; Shen et al., 2019) and the association between RTD and LDMC; Bergmann et al., 2017; Shen et al., 2019).

It is important to recognize, however, that these relationships are not always evident. Indeed, recent work by Bergmann et al. (2020) and Weigelt et al. (2021) illustrates that the principal gradient among root traits in natural systems often reflects the degree of mycorrhizal collaboration, not classical resource economics. SRL and RD form the endmembers of the mycorrhizal collaboration gradient. This effectively decouples SRL, the plant trait with the largest direct effect on Ksat (Fig. 3), from other resource economics variables, including leaf traits like SLA that are used to characterize plant adaptive strategy. Work thus far suggests that mycorrhizal associations are relatively limited in stormwater bioretention (Winfrey et al., 2017), which may explain the absence of the collaboration gradient from the systems we evaluated (the first principal component across all evaluated root traits was entirely consistent with classical resource economics; see Appendix A, Fig. S1). Given that several research groups are actively pursuing mycorrhizal seeding experiments in stormwater bioretention, however, this may not always be the case (Palacios et al., 2021; Poor et al., 2018). It could become necessary to revisit the collaboration gradient in the future and fully characterize its potential impacts on the utility of adaptive strategy theory for inferring plant effects on Ksat. For the systems evaluated here, however, adaptive strategy theory performed extremely well. Reflecting this, the remainder of this discussion is devoted to insights that emerged from its application and their practical implications for ecological engineering design.

4.1. Plants don't always increase Ksat in stormwater bioretention

Most design manuals focus on the capacity of plants to maintain or enhance infiltration beyond what would be expected by bare filter media (ISWMM, 2020; NCDEQ, 2020). Our results illustrate that not all plants perform this service in stormwater bioretention (see Fig. 2), consistent with observations from natural and agricultural systems (Archer et al., 2002; Lu et al., 2020). Plants with R-type strategies were associated with higher SRL, lower RD, and lower Ksat than bare filter media whereas plants with CS-type strategies were associated with the opposite (Figs. 1–3). This result is consistent with observations by Craine et al. (2001) and Roumet et al. (2006), who found that ruderal plants tend have higher SRL, lower RTD and lower RD than plants with other adaptive strategies, as well as the findings of Lu et al. (2020) that plants with these characteristics tend to block soil pores and eliminate macropores, reducing infiltration. The counter hypothesis posed by Cui et al. (2019) (i.e., that ruderals will have higher root senescence, a consequence of enhanced SRL, creating preferential flowpaths and increasing hydraulic conductivity) is not obviously supported by the results of this study.

4.2. Ruderal species that decrease Ksat could help meet infiltration targets

Hydraulic conductivity in established bioretention cells exceeded design maxima approximately 60% of the time. These upper Ksat limits reflect a variety of considerations, including plant survivorship (if water infiltrates too fast, not enough remains to support plant growth; FAWB, 2009), local climate (limits are often higher in tropical climates than temperate ones; 500 vs 300 mm/h; FAWB, 2009), and effective removal of nutrients and pathogens (limits based on pollutant removal are relatively low; 25.4 mm/h for nitrogen removal and 50.8 mm/h for phosphorous, metals and other pollutants; Hunt and Lord, 2006).

Unexpectedly high Ksat values have been reported in bioretention systems (and media mixes) from around the world (Beryani et al., 2021; Fassman-Beck et al., 2015; Virahsawmy et al., 2014), suggesting that this issue is relatively common (although not ubiquitous – see Le Coustumer et al., 2012). One implication of this, is that ruderal plants that decrease Ksat could actually be valuable members of bioretention plant communities, helping these systems meet infiltration targets. If true, then today's plant selection practices, which exhibit significant anti-ruderal biasing (Fig. 4), should probably be revisited.

Anti-ruderal bias is often informed by concerns about the maintenance burden associated with nuisance weeds and annuals, many of which exhibit ruderal adaptive strategies (Krauss and Rippy, 2022). However, not all ruderals are undesirable. Many are floriferous, producing attractive multicolor displays that if sufficiently self-seeding provide recurrent aesthetic value (Dunnett, 2015; Hoyle et al., 2018; Rippy et al., 2021). Ruderals also are uniquely suited to re-colonize space, preserving plant cover when stress or disturbance causes other species to die back (Dunnett, 2015; Vanstockem et al., 2019). This provides a means for bioretention to self-repair, creating designed, novel ecosystems with the capacity to be self-sustaining (Higgs, 2016). Viewed in this light, and in context with their potential hydrologic benefits, incorporating more ruderals into bioretention plant communities is worth considering.

4.3. Bioretention systems are likely to become more ruderal over time, decreasing Ksat

The majority of bioretention systems evaluated (four of seven) exhibited an increase in ruderal plant species over time (Fig. 6a). If these systems had been stress-dominated we would have expected to observe transitions towards more stress-tolerant plant communities (Grime, 1977; Grime and Pierce, 2012). If stress and disturbance had both been low (evident in only 2 systems; Fig. 6a), we would have expected competitive dominants to thrive (Grime, 1977). Ruderal transitions suggest that disturbance plays a key role in shaping bioretention plant communities in the humid, subtropical climate where this study was conducted (Dunnett, 2015). Transitions towards more ruderal or stress tolerant plant species have been noted previously in other NbS such as green roofs (Catalano et al., 2016; Dunnett, 2015; Köhler, 2006; Lundholm et al., 2014; Thuring and Dunnett, 2019), but to our knowledge this is the first time such transitions have been characterized in bioretention. Disturbance could take on a variety of forms in these systems, including, but not limited to, erosive flows, maintenance activities such as weeding, mowing, or bushhogging of vegetation, grazing by deer or other herbivores, and trampling by people or animals (Beryani et al., 2021; Dellinger et al., 2021; Herzog et al., 2021; Krauss and Rippy, 2022; Mazer et al., 2001).

Because ruderal plants decrease hydraulic conductivity, their recruitment has a measurable effect on hydrologic performance as systems age (see Fig. 6c). As noted in section 4.2, this is not necessarily a bad thing if saturated hydraulic conductivity generally exceeds design targets. None of the systems evaluated here showed any indication of clogging, and some of our older systems had upwards of 40% ruderal cover. However, it is certainly possible that the combined effects of ruderal recruitment and other factors that reduce stormwater infiltration as systems age (e.g., accumulation of fine sediments or soil compaction, often associated with poor pretreatment or maintenance practices; DelGrosso et al., 2019; Ebrahimian et al., 2020; Langergraber et al., 2003), could impair bioretention performance. This could make it worth explicitly planning for plant community transitions as part of the engineering design process.

4.4. Plant effects and filter media effects on Ksat are comparable in mature bioretention systems

The results of our path analysis illustrate that the magnitude of filter media effects, root traits, and plant adaptive strategies (R, CS, and S) on Ksat did not significantly differ in mature bioretention systems (Fig. 3b). This result was somewhat unexpected, given the primacy of soil texture in hydrologic design (Ebrahimian et al., 2020). It is not, however, inconsistent with the literature, where the relative importance of plants and soil characteristics is itself inconsistent, reflecting differences in climate, prior land use, ecosystem age, and the specific plant and soil characteristics evaluated, among other factors (Hao et al., 2020; Lozano-Baez et al., 2019; Thompson et al., 2010; Wang et al., 2023). For instance, work by Hao et al. (2020) found that plant traits like root length density played a greater role in regulating infiltration than soil characteristics (SOM, porosity, etc.) in humid climates like the one evaluated in this study. Thompson et al. (2010), on the other hand found that plants influenced infiltration more than soil texture in arid climates but that the effect became progressively smaller as humidity increased, ultimately reversing in humid-mesic climates. Age of the plant community also plays an important role in moderating the magnitude of observed plant effects, particularly for woody plant species. Indeed, Lozano-Baez et al. (2019) found that mature plant communities exerted significantly more influence over infiltration rates than younger plant communities; Their definition of mature was ≥10 years old, an age exceeded by 60% of the bioretention cells we evaluated. This suggests that plant effects in more recently established bioretention systems might be smaller than those evaluated here, supposing that other mitigating factors (e.g., plant community composition and climate) remain comparable.

Although, the above-noted dichotomy of plants vs soil is conceptually straightforward, in practice these pathways are not always distinct. In our path analysis, median particle size influenced Ksat indirectly though root traits like SRL, and several plant adaptive strategies influenced Ksat through SOM, illustrating a degree of interconnectivity between plants and soils (Fig. 3). Work by Wang et al. (2023), also revealed substantial combined effects of roots and soils on hydraulic conductivity (i.e., accounting for 13–30% of the explainable variance in infiltration rates). Although interdependencies between plants and soils often manifest in the form of differential plant effects on Ksat as a function of soil texture (Houdeshel et al., 2012; Lozano-Baez et al., 2019; Silver et al., 2000; Wang et al., 2023), there was relatively weak evidence for this in our study. Adaptive strategy effects on Ksat were largely similar in bioretention cells with different media types, differing only for S and CS-type plants (higher impact in sand; Appendix A, Fig. S2). This could reflect the range of soil textures evaluated here, and in bioretention systems more generally, which is narrower than the range over which such relationships are typically evident (i.e., sandy soils to clays; see Lozano-Baez et al., 2019).

4.5. *Planting guidance (and adherence to it) moderates plant effects on Ksat in different climates*

If we presume for a moment that planting guidance will be followed in each climate zone and that the relationships observed here between plant adaptive strategy and Ksat will remain similar across climates (both big assumptions), then we'd expect to see more C and CSR-type plants in bioretention from humid climates, with minimal impact on Ksat, and more CS and S-type plants in bioretention from arid and warm Mediterranean climates, generally increasing Ksat (Fig. 5). Prioritizing plants with minimal influence over Ksat in humid-continental climates places the majority of the burden for managing infiltration on initial media selection in regions where the water volumes being managed are relatively large (Weathers et al., 2023). This is not necessarily a problem if appropriate media is used, but plants are unlikely to help compensate in instances where it is not (i.e., functional redundancy is relatively low).

Prioritizing plants that increase Ksat in arid climates has the potential to be more problematic because it could reduce plant available water (and exacerbate water stress) in regions where plants are already water limited (Houdeshel et al., 2012). Design modifications exist that could mitigate this problem such as internal water storage zones (gravel storage layers that are situated below filter media and provide supplemental water to vegetation; Houdeshel et al., 2012; Li et al., 2014). There is concern, however, that their effectiveness may be limited under climate change; Accommodating extreme storms is expected to require deeper filter media (Tirpak et al., 2021; Weathers et al., 2023), which could push internal water storage zones out of reach of all but the deepest-rooted plant species. This eventuality would make it necessary to revisit current planting practices.

As we consider the implications of our climate-specific projections of plant effects, its important to circle back to the initial assumptions upon which they are based (i.e., relationships between adaptive strategy and Ksat will be comparable across climates and planting guidance will be followed), neither of which we expect are strictly true. In section 4.4 we highlighted several instances where plant effects on infiltration have been observed to vary with climate (e.g., Thompson et al., 2010). Furthermore, we observed clear differences between recommended and actual planting practices in climate zone CFA that significantly altered both plant adaptive strategy and Ksat (see Figs. 4 and 5e). Both lines of evidence suggest that our plant effect projections in Fig. 5 should be interpreted with caution. They are first and foremost hypotheses, and we hope that they will be leveraged as such to generate new thought experiments, serve as a starting point for debate, and perhaps inspire new climate-specific studies that explore the utility of plant adaptive strategy for managing Ksat in different regions.

5. Conclusions

This study illustrates that adaptive strategy theory has the potential to be a useful overarching framework for understanding how plants influence soil hydraulic properties such as Ksat in stormwater bioretention. Ksat varied significantly with plant adaptive strategy, with S and CS-type plants tending to increase Ksat relative to bare filter media and R-type plants tending to decrease it, bringing conductivity measurements (which were relatively high) more in line with infiltration targets (Fig. 2a). Plant adaptive strategy was found to impact Ksat indirectly (i.e., through other plant and soil variables), making its effect on Ksat somewhat weaker than root traits or filter media characteristics, but not significantly so (Fig. 3a). Indeed, total plant and filter media effects on Ksat were statistically comparable in mature bioretention systems (Fig. 3b). When considered collectively, these results illustrate both the value of factoring plants into the hydrologic design process for bioretention and the viability of adaptive strategy theory as an ecological design tool for doing so.

The relationships between plant adaptive strategy and Ksat elucidated here appear to have both spatial and temporal implications for hydrologic performance. Plant effects on Ksat are likely to vary over time in response to ruderal recruitment, which occurs more often than classical succession (e.g., competitive dominance), and can be expected to reduce Ksat up to 15 % (Fig. 6). Plant effects on Ksat are also projected to vary geographically because current planting guidance recommends plants with different adaptive strategies (and therefore potential to influence Ksat) in arid versus humid climate zones (Fig. 5; Krauss and Rippy, 2022). These projections are extremely sensitive to small biases in planting preferences (Figs. 4, 5e), illustrating that relatively minor decisions made by us can have outsized hydrologic impacts.

Although we have been careful to ensure that the findings reported above are statistically robust, its important to remember that they reflect work completed on a relatively small subset of bioretention systems (fifteen), from a single climate zone. Fully characterizing the utility of adaptive strategy theory as a tool for understanding plant effects on Ksat will require additional evaluation of bioretention systems from other climates and their native plant communities. Given the prominence of the mycorrhizal collaboration gradient in natural systems (Bergmann et al., 2020; Weigelt et al., 2021), and its potential to disrupt relationships between plant adaptive strategy and Ksat, it will also be important to compare the utility of adaptive strategy theory in bioretention with engineered media to systems with natural soils, providing a more complete picture of adaptive strategy theory's strengths and weaknesses for ecological engineering design.

Part of painting this more complete picture will be looking beyond Ksat and thinking more broadly about the range of services adaptive strategy might influence. This could start small, looking more deeply at other ways plants influence stormwater capture in bioretention (e.g., via plant water uptake and evapotranspiration), both of which have been linked to plant adaptive strategy through the fast-slow plant economic spectrum (Payne et al., 2018; Schrieke and Farrell, 2021). It could also involve casting a much broader net, looking at the implications of various strategies for pollutant removal, carbon sequestration, thermal regulation, biodiversity, and cultural services like aesthetics (Krauss and Rippy, 2022; Le et al., 2023). Doing so could help us frame plant selection and ecological design more holistically (i.e., highlighting tradeoffs as well as synergies across the services plants influence), and ultimately set the stage for more multifunctional bioretention designs.

CRediT authorship contribution statement

L. Krauss: Data curation, Formal analysis, Visualization, Writing – review & editing. **M.A. Rippy:** Conceptualization, Methodology, Formal analysis, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2023.107148.

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