

Heteromorphic characteristics of *Bidens pilosa* (Asteraceae) achenes influence adherence stability and dispersal capacity

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Abstract. Seed dispersal away from the parent plant is paramount for angiosperms to reduce intraspecific competition, as well as predation and disease risks. The ability to disperse seeds over long distances can contribute to the colonisation of new habitats and places, which sometimes causes problems for humans. Species with such dispersal capabilities may consequently be considered invasive. Seed dispersal strategies can vary between and within species. Some species, such as the weedy *Bidens pilosa* (Asteraceae), exhibit heteromorphism in their fruits (achenes). Being dispersed by animals, the achenes vary in size, rugosity and number of barbs even within each infructescence, all of which can potentially influence adherence stability to the hair, fur and clothes of the dispersers. Studying these morphological traits thus allows us to examine if and how they might predict the dispersal capacity of the achenes. A total of 326 achenes from 56 *Bidens pilosa* infructescences were measured then subjected to a spring test to test for adherence. Two achene types—peripheral and central—are distinguishable by six measured traits, particularly the achene length and fruit width. We found that the adherence stability of achenes is affected by the number of barbs and barb lengths. Longer two-barbed achenes and shorter three-barbed achenes fully adhere better than shorter two-barbed achenes and longer three-barbed achenes, respectively. Longer barbs and slenderer fruits also contribute to better hanging of the achenes on the cloth surface. Our study demonstrates that achene traits are useful in predicting adherence stability and hence dispersal capacity.

Key words. adaptation, exotic, life form and function, non-native, seed dispersal, trait

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INTRODUCTION

Seed dispersal is important for angiosperms. Ensuring that future generations germinate as far away as possible from their parent plants can reduce intraspecific competition as well as lower predation risk and pathogen infection events (Wenny, 2001), and also allow the species to colonise new areas (Howe & Smallwood, 1982; Cain et al., 2000). Plants adopt various seed dispersal strategies such as the use of gravity, wind, water and animals, or ballistic force. Different species have adapted to exhibit different seed morphologies and traits to maximise seed dispersal ability (Howe & Smallwood, 1982; Cain et al., 2000; Schupp et al., 2010). Intraspecific variations in seed morphology and physiology, particularly among polymorphic species, can also have consequences on the population dynamics and interactions with other sympatric species (Truscott et al., 2006; Clements & Ditommaso, 2011). This is particularly relevant when the environment undergoes changes. Consequently, studying seed dispersal is critical to understanding ecological evolution and microevolutionary processes as well as community interactions (Schupp et al., 2010).

Some plants have also adapted to dispersal with the help of humans (Von Der Lippe et al., 2013; Auffret et al., 2014). In this era of globalisation, these plants can easily spread to places that are not possible for them to reach naturally. When they start to establish themselves in a novel environment, they can sometimes become invasive, driving ecological changes through habitat degradation, lowering native biodiversity, altering ecosystems and changing the evolutionary trajectories of species (Roux & Wicczorek, 2009). Species invasions not only cause harm to the local ecosystem, but can also incur substantial economic and social costs (Pimentel et al., 2005).

To better manage weeds, more attention has to be placed on examining the functional trait ecology of these plants (Woo et al., 2020). Specifically, investigation of seed traits can be particularly useful to understand how species, population and individual differences in morphology and traits can predict and influence seed dispersal (Woo et al., 2020). This is especially so as invasive plants are known to exhibit higher levels of phenotypic plasticity, resulting in differences in dispersal, germination and post-germination adaptive behaviour (Davidson et al., 2011). This allows them to employ a bet-hedging strategy to cope with novel environments and compete with established vegetation (Venable, 1985; Davidson et al., 2011).

Fruit and seed heteromorphism are types of phenotypic plasticity where a genotype produces multiple morphophysiological seed forms (Imbert, 2002). These seed forms not only differ in visual appearance (i.e., size and mass [Rocha, 1996]), but also in dispersal ability (Rocha, 1996; Zhang et al., 2015), dormancy and germination (Zhang et al., 2015; Zhang et al., 2019). Consequently, such heteromorphism increases the plant's adaptability in novel and heterogenous environments (Baskin & Baskin, 2014). This phenomenon is particularly prominent in weeds and has been well documented in species of the family Asteraceae (Imbert, 2002). In a study investigating heteromorphic plants, 63.6% of the species (52.5% of the genera) belong to the Asteraceae (Imbert, 2002), with many of them producing two seed forms (Rocha, 1996). Species from the family Asteraceae produce a capitulum or head consisting of a cluster of flowers (Fig. 1A). They develop into infructescences (fruiting heads; Fig. 1B), of which the individual fruit containing the seed is termed an achene (Fig. 1B).

Bidens pilosa L., a plant native to the disturbed areas or open ground in tropical or subtropical Central America, is considered one of the most invasive plants in the world and now widely distributed in the tropics and subtropics (Reddy & Singh, 1992; USDA, NRCS, 2021). The achenes are dispersed by animals, and typically have two or three awns (also known as barbs; Fig. 1C) that enable them to cling to the fur and feathers of browsing fauna, as well as to human clothing. The achenes of *Bidens pilosa* are dimorphic and can be classified into central and peripheral achenes based on the surface of the fruit wall (pericarp) (Rocha, 1996; Zhang et al., 2019).

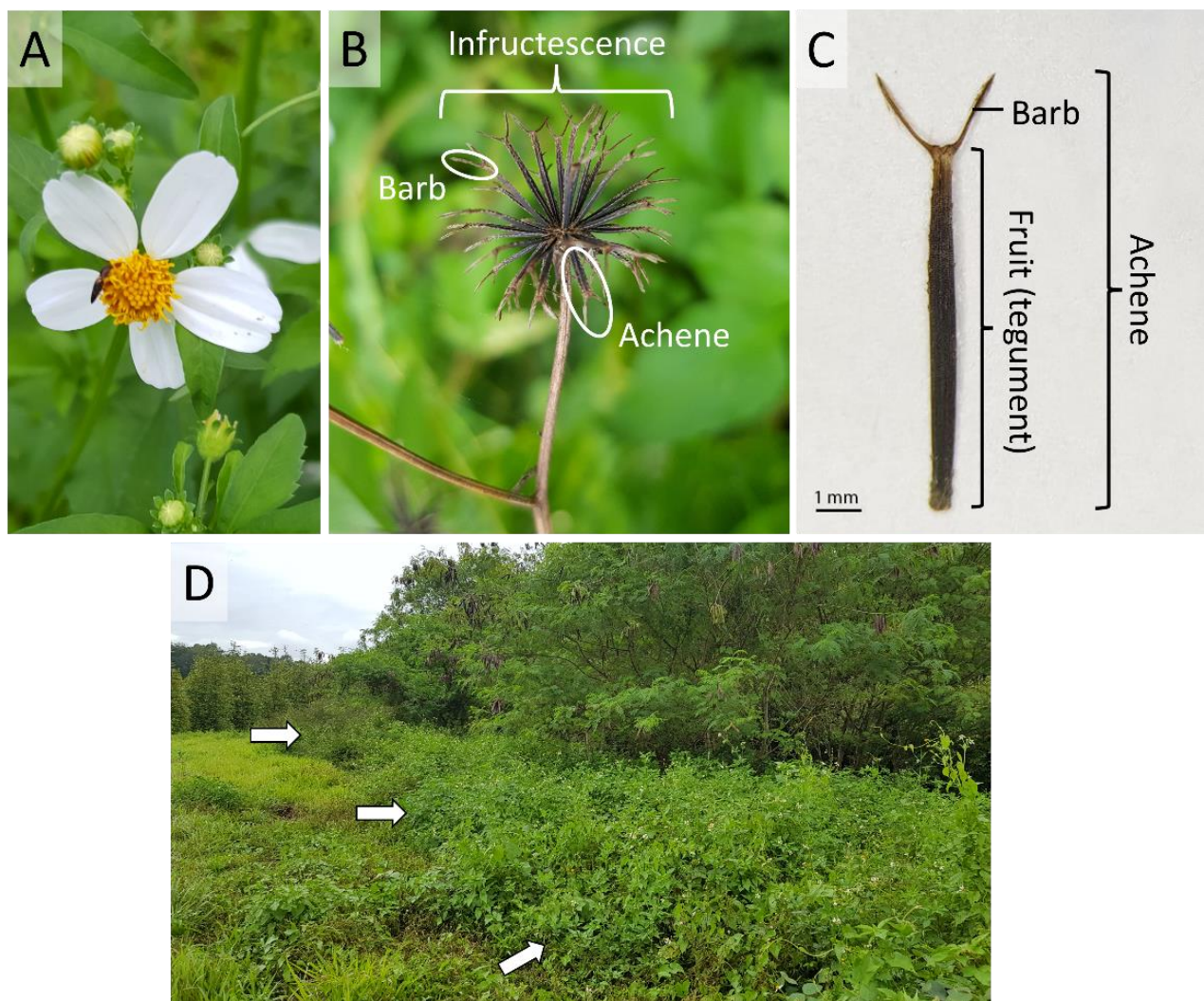


Fig. 1. *Bidens pilosa*. A, capitulum; B, intact infructescence; C, an achene with corresponding terminology used in this study. D, area along Lorong Lada Hitam, Singapore, where *Bidens pilosa* infructescences (white arrows) were sampled.

In *Bidens pilosa*, dispersal capacity is influenced by the ability of the achenes to attach stably to the outer covering of the disperser (e.g., fur of mammals, feathers of birds and/or clothing of humans). Certain achene traits, such as longer barb length or a more rugulose pericarp surface, may enable the achene to stay attached to the surface of the dispersal agent for a longer period of time before dropping off, thereby enabling this species to disperse further and colonise previously unoccupied areas.

Although several trait studies on the achenes of *Bidens pilosa* have been conducted (e.g., Amaral & Takaki, 1998; Hao et al., 2009; Zhang et al., 2019), we are unaware of any study that employs multivariate analyses to investigate a suite of achene traits and how the traits might predict dispersal capacity holistically in an experimental setup. Here, we investigated achene variation in a local population of *Bidens pilosa*, which is non-native to Singapore, and explored if these morphological traits affect dispersal capacity of the achenes. Specifically, we aimed to address the following questions: (a) What is the trait variation of Singapore *Bidens pilosa* achene heteromorphism? (b) Does achene trait variation play a role in dispersal capacity by influencing attachment stability during seed dispersal?

MATERIAL & METHODS

Collection of materials. *Bidens pilosa* can be found in abundance among open fields in Mandai, Singapore (Fig. 1D). Infructescences from one population of *Bidens pilosa* were collected from a wasteland at Lorong Lada Hitam (1°25'06.9"N, 103°47'31.5"E). Only fully developed, complete infructescences were collected from the same day. As it was not possible to ascertain if the infructescences were taken from different individual plants, we sampled within a 100-m radius to minimise confounding effects such as age of infructescences, generation and population and individual differences. Each infructescence was cleanly cut off at the peduncle and placed singly in a small vial, and care was taken to ensure that the achenes were not dislodged. If too many achenes were lost, the infructescence was discarded. In total, 57 infructescences were used for trait measurements and experiments.

Trait measurements. To measure the achene traits, achenes were gently removed using a pair of fine forceps and classified as central or peripheral achenes by observing the surface of the pericarp. Peripheral achenes have a more verrucose pericarp surface than central achenes (Amaral & Takaki, 1998) (Fig. 2B). Damaged achenes were discarded. Three central and three peripheral achenes from each infructescence were randomly selected for trait measurements and experiments. For each achene, the achene length (acheneLength), fruit length (fruitLength), fruit width (fruitWidth) and barb lengths (barbLength) (Fig. 1C) were measured using a 6-inch VIS vernier caliper (1/20 mm). The number of barbs on each achene was also recorded. The weight of each achene was measured using a Quintix® Semi-Micro Balance (Satorius AG, Germany).

All statistical analyses were carried out in R (R Core Team, 2020). To investigate the distribution of achene traits between the two different types of achenes across all the sampled infructescences, a Principal Component Analysis (PCA) was carried out using the R function 'prcomp'. As the achene traits were not mutually independent and likely to be highly intercorrelated, they were summarised into major gradients of variation. Permutational multivariate analysis of variance (PERMANOVA) with 999 permutations, using the Euclidean method, was performed using function 'adonis' from the community vegan package to test for differences in morphological traits among central and peripheral achenes (Oksanen et al., 2019).

Test for adherence stability of achenes. To examine whether the traits predict adherence stability of the achenes, an experiment was carried out (Fig. 2). A Pesola light-line scale spring was clamped to a retort stand and a 2.8 × 2.8 × 2.8-cm melamine sponge with cloth wrapped around it was fixed to the spring. A piece of cotton organdy cloth was chosen as it resembles human clothing and provided a standardised medium for the achenes to attach to. A spring test was carried out by lightly pressing an achene (without damaging the achene) to the cloth with the length of the achene parallel to the surface, and pulling the spring to 700 g and releasing it, to examine how well different achenes attach to the surface. A force of 700 g was chosen as preliminary trials showed that this was sufficient to dislodge some but not all of the achenes. Whether the achene was fully adhered to the cloth, partially hanging off but attached at the barbs, or had dropped off entirely, was recorded.

To investigate the influence of various achene traits on the extent of adherence stability of fruits and achenes, the data were separated into two datasets for separate analyses, respectively: Dataset 1, comprising achenes which were fully adhering (barbs and fruit attached) to the cloth vs. achenes which were partially hanging off (i.e., fruit detached but barb[s] attached to the cloth); and Dataset 2, comprising achenes which were partially hanging off (i.e., fruit detached but barb[s] attached to the cloth) vs. achenes which had dislodged entirely. Generalised linear mixed-effects models (GLMMs) with binomial error structure were fitted using the function 'glmer' from package 'lme4' (Bates et al., 2015) to model the outcomes of the spring test as a binary response. As more than one achene was used from each infructescence, the identity of the infructescence was used as a random intercept. A total of 51 models for each dataset containing different combinations of the traits, including single effects (e.g., ~ acheneLength), additive effects (e.g., ~ acheneLength + fruitWidth) and interactive effects (e.g., ~ acheneLength × fruitWidth) were proposed and ranked according to the Akaike Information Criterion corrected for small sample sizes (AICc) using the 'MuMIn' package (Barton & Barton, 2015). A null model (~ 1) was also included. The cut-off for model averaging was delta (difference between the AICc of a particular model and that of the best model) less than 2.0 (Burnham & Anderson, 2002).

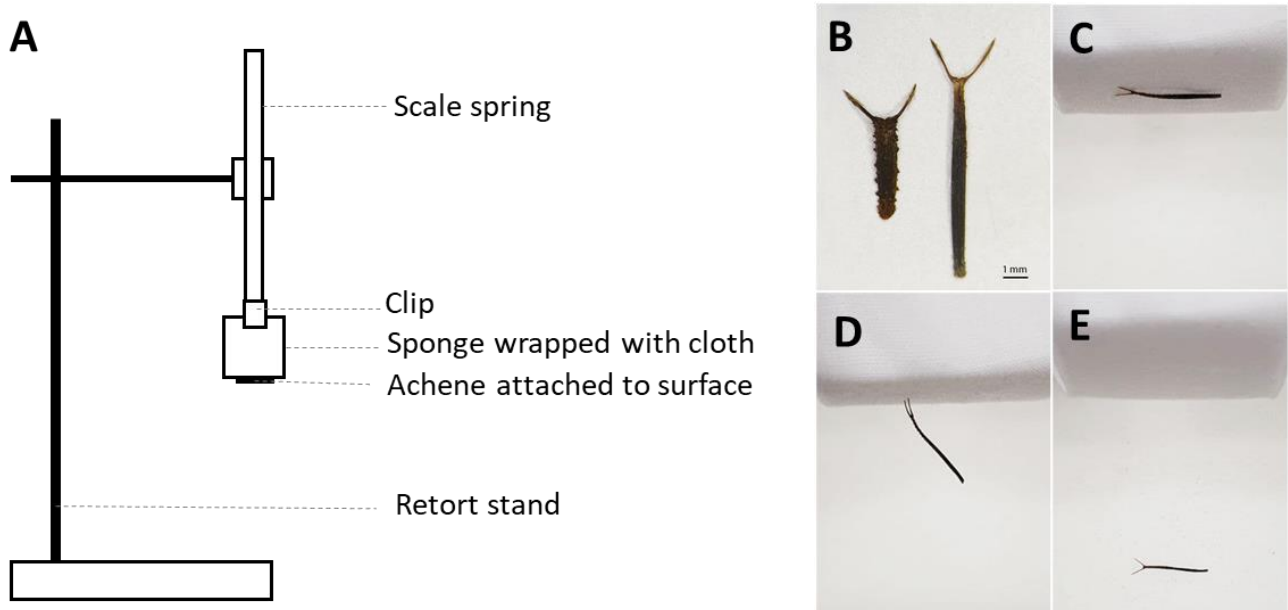


Fig. 2. A, experimental setup of the spring test. B, *Bidens pilosa* peripheral (left) and central achenes (right). After conducting the spring test, the achenes were scored as fully adhering (C), hanging off (D) or entirely dislodged (E) from the setup.

RESULTS

A total of 326 achenes from 56 *Bidens pilosa* infructescences were subjected to the spring test. Of the 329, 118 were fully adhered to the setup at the end of the test, 68 were hanging off by the barbs, and 143 had dropped from the setup. The achenes also differed in number of barbs, with most of them being two-barbed ($n = 301$). Among achenes with three barbs ($n = 26$), 14 were peripheral and 12 were central achenes. These achenes were from 13 infructescences, which had a mixture of two- and three-barbed achenes.

The first and second PC axes explained 37.8% and 22.1% of the variation, respectively, accounting for 59.9% of total variation (Fig. 3A). The two achene types—peripheral and central—were distinguishable by the six measured traits (PERMANOVA F-value = 280.6, $R^2 = 0.46$, p-value = 0.001) (Fig. 3A). Specifically, there was a significant difference in the achene length (which also correlated with fruit length) between central ($M = 10.39$) and peripheral achenes ($M = 7.64$, t-value = 18.6, p-value < 0.001, 95% CI [2.5, 3.0]). Fruit width also differs significantly between the central ($M = 0.84$) and peripheral achenes ($M = 1.03$, t-value = -7.4, p-value < 0.001, 95% CI [-0.24, -0.14]) (Fig. 3B). The two types of achenes did not differ significantly by weight (t-value = 0.763, p-value > 0.05, 95% CI [-0.04, 0.08]).

In comparing achenes which were fully adhering or partially hanging off (Dataset 1), model selection by AICc indicated that the two best models contained fruit width and the interaction between number of barbs and mean barb length as predictors (Table 1). In both models, larger achenes with two barbs were more likely to stay fully attached to the cloth after the spring test, but smaller achenes with three barbs were also likely to stay attached to the cloth (estimate = -1.43 ± 0.66 , 95% CI [-3.04, 0.31]) (Fig. 4A). Fruit width had a weak effect on the probability of the achenes attaching to the cloth after the spring test (estimate = 0.35 ± 0.19 , 95% CI [0.00, 0.73]).

Comparing between achenes which were partially hanging off or which had dropped off entirely (Dataset 2), model selection by AICc indicated three best models containing mean barb length, and two best models containing fruit width as weak predictors (Table 2). In all three models, achenes with longer mean barb length were more likely to hang on to the cloth (estimate = 0.39 ± 0.19 , 95% CI [0.01, 0.79]) (Fig. 4B). Achenes with smaller fruit width were more likely to hang on to the cloth after the spring test (estimate = -0.41 ± 0.2 , 95% CI [-0.82, -0.03]).

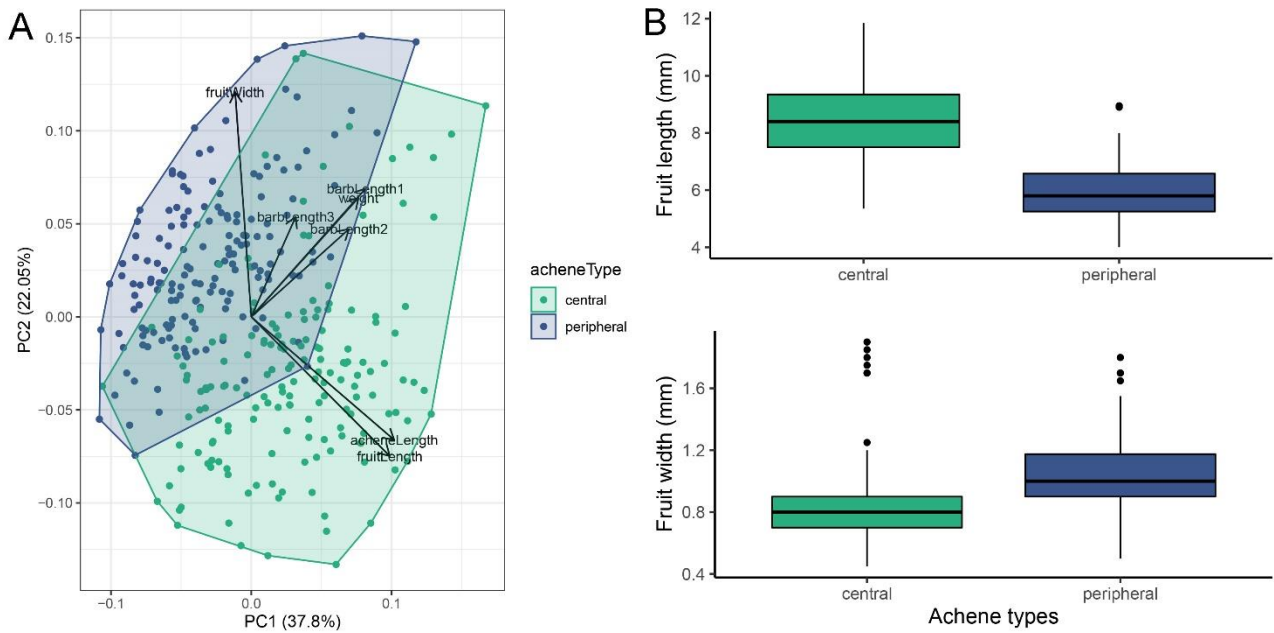


Fig. 3. A, Principal Component Analysis (PCA) summarising the six measured traits of the *Bidens pilosa* central and peripheral achenes, accounting for 59.9% of the variance. B, boxplots visualising the difference in fruit length and width between central and peripheral achenes; whiskers represent the minimum and maximum values; the lower border, thick line and upper border of the box indicate the first quartile, median and third quartile, respectively.

Table 1. Summary for the first five models of the traits that predict the probability of *Bidens pilosa* achenes remaining fully attached to the cloth during the spring test using Dataset 1. All models contain infructescence ID as random effect. Note that all continuous predictors were scaled. d.f. refers to the degree of freedom; Weight refers to relative likelihood of a model; R^2_m and R^2_c refer to the marginal and conditional R^2 respectively.

Models	Intercept	d.f.	AICc	Delta	Weight	R^2_m	R^2_c
~ numBarbs × MbarbLength + fruitWidth	-0.9	6	239.9	0.00	0.27	0.10	0.14
~ numBarbs × MbarbLength	-1.7	5	241.4	1.52	0.13	0.08	0.13
~ numBarbs + fruitWidth	3.1	4	242.3	2.45	0.08	0.05	0.09
~ numBarbs × fruitWidth	4.0	5	242.4	2.56	0.08	0.07	0.11
~ numBarbs × MbarbLength + fruitLength	-1.5	6	242.8	2.89	0.06	0.08	0.14

Table 2. Summary for the first five models of the traits that predict the probability of *Bidens pilosa* achenes hanging on to the cloth during the spring test using Dataset 2. All models contain infructescence ID as random effect. Note that all continuous predictors were scaled. d.f. refers to the degree of freedom; Weight refers to relative likelihood of a model; R^2_m and R^2_c refer to the marginal and conditional R^2 respectively.

Models	Intercept	d.f.	AICc	Delta	Weight	R^2_m	R^2_c
~ numBarbs × MbarbLength + fruitWidth	4.9	6	255.4	0.00	0.184	0.10	0.25
~ MbarbLength + fruitWidth	-0.9	4	256.7	1.36	0.093	0.05	0.20
~ numBarbs × MbarbLength	5.3	5	256.9	1.57	0.084	0.08	0.24
~ acheneType + fruitWidth + MbarbLength	-1.1	5	258.2	2.81	0.045	0.06	0.20
~ fruitWidth + weight	-0.9	4	258.2	2.85	0.044	0.04	0.21

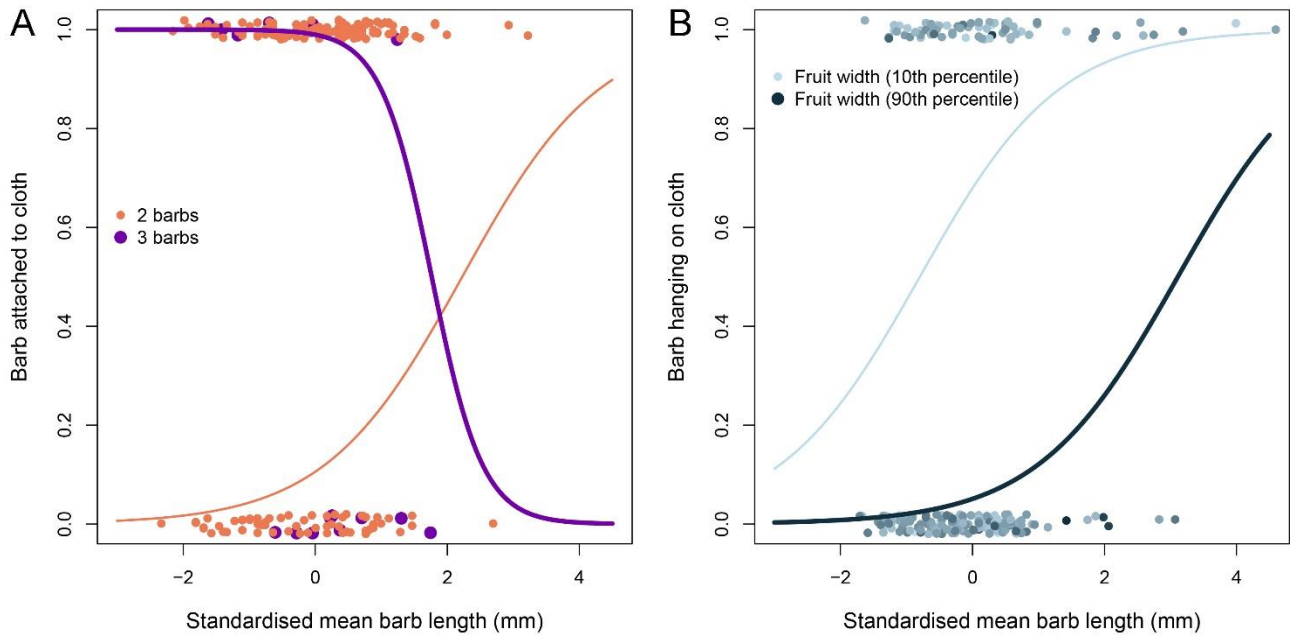


Fig. 4. Binomial regression plots. A, plot showing the association of mean barb lengths and number of barbs with the spring test outcome in Dataset 1; the dots represent the binary outcome of the two-barbed (orange) and three-barbed (purple) achenes, where ‘1’ indicates that the achene remained fully adhered to the cloth and ‘0’ means the achene was hanging off. B, plot showing the association of mean barb lengths and fruit width with spring test outcome in Dataset 2; the dots are represented with different colours along a gradient, with light to dark shades representing achenes with increasing fruit width; ‘1’ indicates that the achene was hanging off the cloth and ‘0’ means the achene was dislodged entirely.

DISCUSSION

To inhabit and thrive in unpredictable environments, many plant species have evolved a variety of morphological and physiological adaptations to increase fitness to survive better (Harper et al., 1970; Hughes, 2018). The present study has corroborated that *Bidens pilosa* produces two types of achenes (central and peripheral) with variations in traits such as barb length, fruit width and weight. These traits can influence the ability of achenes to adhere stably to a dispersal surface and may thus affect dispersal capacity. The variations in these achene traits may enable *Bidens pilosa* exhibiting achene heteromorphism to maintain different adaptive dispersal strategies and contribute to the successful survival of this species.

The multivariate analysis demonstrated that central and peripheral achenes from *Bidens pilosa* in Singapore can be broadly differentiated based on the six measured traits. Central achenes are typically longer and thinner than peripheral achenes. This has been observed in *Bidens pilosa* achenes from both its native range in Costa Rica (Rocha, 1996) and invasive range in China (Zhang et al., 2019). The mean weights of central and peripheral achenes in Singapore were not found to be significantly different, however, which contrasts with previous studies showing that central achenes are significantly heavier than peripheral achenes (Rocha, 1996; Zhang et al., 2019). Achene weight could be an indication of differential resource allocation in heteromorphic achenes, resulting in different dormancy periods and germination rates (Forsyth & Brown, 1982; Venable & Levin, 1985). As Singapore has a relatively constant and humid environment, the similar weights of both central and peripheral achenes might be an indication that both types of achenes are adapting to an aseasonal climate.

The dispersal capacity of achenes can depend on the ability of the achenes to remain stably attached to the fur or clothing of a dispersal agent. We demonstrated that the adherence stability could be affected by the number of barbs and barb lengths (Fig. 4A). In two-barbed achenes, achenes with longer barbs are more likely to remain fully adhered to the cloth after the spring test. In contrast, three-barbed achenes with longer barbs tend to end up in a hanging position. The presence of a third barb could affect the angle formed by the other two barbs and reduce the amount of achene surface available for attachment. The additional barb may also create a more stable tripod position when hanging off the cloth as compared to when fully adhered. This imbalance could be further aggravated by longer barb lengths. In two-barbed achenes, the longer barb lengths may help to increase the ability of the achene to adhere fully to the setup by bringing the fruit into contact with the cloth.

The probability of being entirely dislodged increases in achenes with shorter barbs and greater fruit widths, regardless of the number of barbs (Fig. 4B). This can be attributed to shorter barbs not being able to hook as effectively on to the cloth fibres, and wider fruits possibly worsening overall instability. Interestingly, peripheral achenes differed from central achenes in fruit width but not barb length, suggesting that peripheral achenes are not necessarily less effective in dispersal than central achenes.

There are other achene traits that may also influence the dispersal capabilities of the achenes. These include degree of rugosity, angle and curvature of barbs, as well as the morphology of hooks on the barbs; but they are not easily quantified and analysed. Environmental pressures can also be an important extrinsic predictor of dispersal capacity. For example, dispersal capacity can differ markedly between the rainy and drier seasons because the amount of water available can modify the overall morphology of the achenes and extent of heterogeneity, as shown in other Asteraceae (De Clavijo, 2002). Given that floral traits of *Bidens pilosa* from Singapore have been reported to exhibit population differences (Tan & Tan, 2018), it is highly likely that the achene traits also differ among populations. Studying more traits along with the environmental variables that each population is subject to over different seasons can therefore reveal novel insights into the adaptive capabilities of this widespread Asteraceae species.

Based on the spectrum of studies on *Bidens pilosa* and related family members, the morphology of the achenes can be seen to be highly heteromorphic and plastic (Rocha, 1996; Zhang et al., 2019; Woo et al., 2020), contributing to various dispersal strategies and likely aiding the success of the species in colonising new environments. However, much less is known about differential resource investment in achene traits and seed physiology, and whether there is any fitness trade-off between dispersal capabilities and survival rates. Furthermore, as we could not ascertain whether the infructescences were collected from different or same plant individuals, inferences could not be made about differences in achene traits within and between individual plants through our study. Measuring achene traits from individually planted *Bidens pilosa* under greenhouse conditions controlled for individual differences and environmental influence can be considered for future investigations. Coupled with physiological investigations, these studies can offer insights into plant resource allocation, especially in weeds such as *Bidens pilosa*, which have proven to be widespread and adaptable in varying environmental conditions.

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LITERATURE CITED

- Amaral A & Takaki M (1998) Achene dimorphism in *Bidens pilosa* L. (Asteraceae) as determined by germination test. *Brazilian Archives of Biology and Technology*, 41: 10–15.
- Auffret AG, Berg J & Cousins SA (2014) The geography of human-mediated dispersal. *Diversity and Distributions*, 20: 1450–1456.
- Barton K & Barton MK (2015) MuMIn: Multi-Model Inference (v.1.43.17). <https://CRAN.R-project.org/package=MuMIn> (Accessed 11 February 2022).
- Baskin CC & Baskin JM (2014) *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. 2nd Edition. Elsevier/Academic Press, San Diego, California, 665 pp.
- Bates D, Maechler M, Bolker B & Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67: 1–48. DOI: 10.18637/jss.v067.i01
- Burnham KP & Anderson DR (2002) *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach*. 2nd Edition. Springer-Verlag New York, USA, xxvi + 488 pp.
- Cain ML, Milligan BG & Strand AE (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany*, 87: 1217–1227.
- Clements DR & Ditommaso A (2011) Climate change and weed adaptation: Can evolution of invasive plants lead to a greater range expansion than forecasted? *Weed Research*, 51: 227–240.
- Davidson AM, Jennions M & Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology letters*, 14: 419–431.
- De Clavijo ER (2002) Role of within-individual variation in capitulum size and achene mass in the adaptation of the annual *Centaurea eriophora* to varying water supply in a Mediterranean environment. *Annals of Botany*, 90: 279–286.
- Forsyth C & Brown NAC (1982) Germination of the dimorphic fruits of *Bidens pilosa* L. *New Phytologist*, 90: 151–164.
- Hao J, Liu Q & Qiang S (2009) Reproductive traits associated with invasiveness in *Bidens pilosa* (Asteraceae). *Chinese Bulletin of Botany*, 44: 656.
- Harper JL, Lovell DH & Moore KG (1970) The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, 1: 327–351.
- Howe HF & Smallwood J (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13: 201–228.
- Hughes PW (2018) Minimal-risk seed heteromorphism: Proportions of seed morphs for optimal risk-averse heteromorphic strategies. *Frontiers in Plant Science*, 9: 1412.
- Imbert E (2002) Ecological consequences and ontogeny of seed heteromorphism. *Perspectives in Plant Ecology, Evolution and Systematics*, 5: 13–36.

- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E & Wagner H (2019) vegan: Community Ecology Package (v.2.5-6). <https://CRAN.R-project.org/package=vegan> (Accessed 11 February 2022).
- Pimentel D, Lach L, Zuniga R & Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, 52: 73–288.
- R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org> (Accessed 11 February 2022).
- Reddy KN & Singh M (1992) Germination and emergence of hairy beggarticks (*Bidens pilosa*). *Weed Science*: 195–199.
- Rocha OJ (1996) The effects of achene heteromorphism on the dispersal capacity of *Bidens pilosa* L. *International Journal of Plant Sciences*, 157: 316–322.
- Roux JL & Wicczorek AM (2009) Molecular systematics and population genetics of biological invasions: Towards a better understanding of invasive species management. *Annals of Applied Biology*, 154: 1–17.
- Schupp EW, Jordano P & Gómez JM (2010) Seed dispersal effectiveness revisited: A conceptual review. *New Phytologist*, 188: 333–353.
- Tan MK & Tan HTW (2018) Asterid ray floret traits predict the likelihood of florivory by the polyphagous katydid, *Phaneroptera brevis* (Orthoptera: Phaneropterinae). *Journal of Economic Entomology*, 111: 2172–2181.
- Truscott AM, Soulsby C, Palmer SCF, Newell L & Hulme PE (2006) The dispersal characteristics of the invasive plant *Mimulus guttatus* and the ecological significance of increased occurrence of high-flow events. *Journal of Ecology*, 94: 1080–1091.
- USDA, NRCS (2021) *Bidens pilosa* L. The PLANTS Database. National Plant Data Team, Greensboro, NC, USA. <https://plants.usda.gov/core/profile?symbol=BIPI> (Accessed 26 March 2021).
- Venable DL (1985) The evolutionary ecology of seed heteromorphism. *American Naturalist*, 126: 577–595.
- Venable DL & Levin DA (1985) Ecology of achene dimorphism in *Heterotheca latifolia*. *Journal of Ecology*, 73: 133–145.
- Von Der Lippe M, Bullock JM, Kowarik I, Knopp T & Wichmann M (2013) Human-mediated dispersal of seeds by the airflow of vehicles. *PloS ONE*, 8: e52733.
- Wenny DG (2001) Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecology Research*, 3: 37–50.
- Woo S, Lee D, Cho YC, Lee S & Kim E (2020) Differential responses to fertilization and competition among invasive, non-invasive alien, and native *Bidens* species. *Ecology and Evolution*, 11: 516–525.
- Zhang K, Baskin JM, Baskin CC, Yang X & Huang Z (2015) Lack of divergence in seed ecology of two Amphicarpeae (Fabaceae) species disjunct between eastern Asia and eastern North America. *American Journal of Botany*, 102: 860–869.
- Zhang K, Yao L, Zhang Y & Tao J (2019) Achene heteromorphism in *Bidens pilosa* (Asteraceae): Differences in germination and possible adaptive significance. *AoB Plants*, 11: plz026.