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Comparison of estimated and experimental subaqueous seed transport

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ABSTRACT

We compare the estimates from the relative bed stability (RBS) equation that indicates incipient bed movement, and the inertial settling ('Impact') law and Wu and Wang (2006) settling velocity equations that indicate suspended particle movement, to flume and settling velocity observations to confirm the utility of the equations for subaqueous hydrochory analyses, and to calibrate our estimates by examining the method by which seed volume is obtained. Comparison of the observed measures with the estimates of the inertial settling ('Impact') law and RBS equations indicate that these two equations appear to provide reasonable approximations of the velocities required to achieve transport both in suspension and on the bed, respectively. The use of the water displacement method for volume measurement is a technologically simple method for improving the accuracy of the estimates. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS seed dispersal; suspended load; bedload; settling velocity; critical velocity

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INTRODUCTION

Subaqueous hydrochory, the movement of non-buoyant seeds by hydraulic processes below the water surface, has gained recognition over the past decade as a potentially important primary seed dispersal mechanism of initially non-buoyant seeds, or secondary movement of seeds that have lost buoyancy (Merritt and Wohl, 2002; Boedeltje *et al.*, 2003; Gurnell *et al.*, 2007, 2008). Markwith and Leigh (2008) took initial steps to understand the flow conditions under which seed movement below the stream surface may be initiated and sustained with open-channel hydraulic modeling. Various common sediment transport equations were used to determine the discharges that produce shear stresses and velocities necessary to move non-buoyant seeds either on the bed or in suspension. Although we had confidence in the conclusions drawn from that analysis, what the methodology did not include was experimental proof that the equations reflect observed effects of streamflow on seeds, and which of the examined equations best estimate observed patterns. The goal of this research note is to compare the estimates from the particle transport equations to empirical observations to establish the simple utility of the equations for subaqueous hydrochory analyses in plant research and management contexts. Also, we hope to calibrate our estimates by examining the method by which seed volume is obtained. The specific research questions include: (1) are the bed and suspended particle transport calculations for seeds supported by controlled observations, and (2) does the water displacement method of seed volume estimation improve the accuracy of the estimates?

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MATERIALS AND METHODS

Sampling locations

A fresh collection of seeds of the species *Hymenocallis coronaria* (J. LeConte) Kunth (Amaryllidaceae) was taken from a population in the Broad River drainage, South Carolina ($n = 53$). *H. coronaria* is an emergent macrophyte that lives in rocky shoals, i.e. rapids, of large rivers of the Piedmont, Ridge and Valley, and Cumberland Plateau provinces of Alabama, Georgia, and South Carolina (Markwith *et al.*, 2009). The seeds of *H. coronaria* are quite large, sometimes reaching lengths greater than 4 cm and diameters of 3 cm, and they are denser than water, median density of $1{\cdot}16$ g/cm^3, and sink in mean flow velocities (Davenport, 1990; Markwith and Leigh, 2008). The stream reach survey utilized for the open-channel hydraulic models is from the Tallapoosa River in the Piedmont of east-central Alabama. HEC-RAS v.3.1.3 (USACE Hydrologic Engineering Center, 2002) step-backwater steady flow analysis was used to model the 0·5-, 1·0-, 1·5-, and 2·0-year return interval flows in the reach. A full species description and further information about the stream survey data and modeling (RP1 reach description) can be found in Markwith and Leigh (2008).

Sediment transport equations

The sediment transport equations and hydraulic modeling procedures were continued unchanged from Markwith and Leigh (2008) (with the exception that the ratio of Shields' dimensionless critical shear stress to channel shear stress is not examined here), and detailed explanations of those equations can be found therein. Equations concerning particle transport on the bed include relative bed stability (Jowett, 1989), which is the ratio of the critical velocity required to just move a particle (V_c) to the predicted water velocity near the bed (V_b). The critical velocity was calculated using the quartz-equivalent diameter of the seeds. A ratio of V_c/V_b less than one indicates that the seed can be moved on the bed by the modeled flow at that cross-section.

The suspension criterion (Allen, 1985) is the ratio of the terminal fall velocity (V_o) of the seeds to the shear velocity (U_τ) calculated by HEC-RAS. Two different equations were used to calculate V_o for each seed, each of which is valid for large particle sizes. The first equation is based on the inertial settling ('Impact') law (V_{oi}) (Rubey, 1933), wherein we us a constant value of 8/3, which lies half way between the 4/3 constant for a particle where all water droplets impacting the particle rebound completely and 16/3 constant for a particle where all droplets are deflected tangentially. The second equation is an updated settling velocity equation (V_{ow}) (Wu and Wang, 2006) that is explicitly related to particle size and shape. Each of these parameters (V_{oi} and V_{ow}) was substituted into the suspension criterion ratio for settling velocity (V_o). A ratio of V_o/U_τ less than one indicates that the onset of suspension can occur due to the modeled flow at that cross-section.

Observational and computational comparisons

Two methods for estimating the volume of the sampled seeds were tested to examine the effect of the seed density parameter on the sediment transport equations. The first method, and the method utilized in Markwith and Leigh (2008), is to calculate seed volume based on the equation for a prolate spheroid [prolate spheroid volume $= 4/3\pi ab^2$, where a is the semi-major axis length (cm) (i.e. half the length), and b is the semi-minor axis length (cm) (i.e. half the diameter)]. The second method is to estimate seed volume by displacement of water in a graduated cylinder (100 ml cylinder with 1 ml increments, and 0·1 measurement precision was recorded). It is well established that the volume of water displaced by a submerged object is equal to the volume of the object.

A flume, with dimensions 15 cm × 30 cm × 183 cm, was used to measure the water velocity necessary to move a seed along the bottom of the flume, simulating transport on a stream bed. Observations were conducted with two bed conditions, a low friction environment with no substrate other than the flume's plexiglass base, and a more realistic friction environment with a coarse gravel bed (i.e. a stable bed at experimental velocities of granitic particle sizes ranging approximately 20–30 mm diameter). A subsample of the collected seeds ($n = 30$) were placed individually on the bottom of the flume and flow velocity was increased until the minimum velocity at which the seed moved through an entire 50 cm reach was recorded. Flume conditions were set at 0·1% slope and 10 cm water depth. Flow velocity was measured with a Flow Mate 2000 Velocity Meter (Marsh-McBirney Inc.) at the end of the reach and 6 cm depth.

Settling velocity was empirically measured by dropping the collected seeds (n = 53) through 1·6 m of water (28·5 °C) in Legion Pool on the UGA campus. Seeds were dropped in front of a metric survey rod, and the process was recorded with waterproof digital video equipment (Pentax Imaging Company). Common digital video software (Quicktime v. 7.6.5) was used for frame by frame analysis (30 frames per second) for each seed settling velocity video. Settling velocity was not measured until each seed had dropped ~1 m, video analysis indicated that the rate of fall was unchanging by that depth.

Statistical analysis included calculation of parameter means and the standard error of the estimated parameters compared to observations. Paired t-tests were used to determine if differences were significant between parameter estimation methods and empirical measurements. Parameter estimates based on the method of estimating seed volume, i.e. the prolate spheroid versus the water displacement methods, were compared for ρ_s (seed density), V_c, V_{oi}, and V_{ow}. The equation-based estimates of V_c were also tested against the low friction (FV_l) and gravel bed (FV_g) flume observations. The estimates of V_{oi} and V_{ow} were compared to the settling velocity observations from legion pool (V_{op}).

RESULTS

Seed density (ρ_s) differs between estimates based on the prolate spheroid volume calculation method and the water displacement method, with the prolate spheroid-based estimate significantly greater (Table I). The critical velocity observations from the two flume environments (FV_l and FV_g) are significantly different, and the two equation-based V_c estimates (i.e. based on prolate spheroid and water displacement methods) are significantly different from each other (Table I). Both FV_l and FV_g are significantly less than the V_c calculation using the prolate spheroid volume estimate. Similarly, FV_l is significantly less than the V_c estimate using the water displacement volume measurement. However, FV_g is significantly greater than V_c using the water displacement volume measurement.

All of the seed parameters, estimated and observed, have means and ranges below the modeled bed velocities along the entire length of all four return interval flows in the Tallapoosa River reach (Figure 1a). Thus, all the seeds can be moved through the entire reach as bedload by flow events as frequent as the 0·5 year return interval flow.

The two V_{oi} estimates (i.e. based on prolate spheroid and water displacement methods) are significantly different from each other, and the two V_{ow} estimates are

Table I. Means, and standard error of the estimates where appropriate, of seed specific parameters calculated with both the prolate spheroid and water displacement seed volume estimation methods, and observed bedload and settling velocities from the flume and pool experiments, respectively. Results from paired t-tests are indicated for comparisons among estimation methods, and among the estimated parameters and observed velocities.

Seed	ρ_s*	V_c*	FV_l*	FV_g*	V_{oi}*	V_{ow}*	V_{op}*
Prolate spheroid method mean (standard error)	1·21	0·25 (0·04, 0·05)[c]	0·06[b]	0·16[b]	31·27 (8·48)[d]	84·43 (22·14)[d]	10.97[b]
Water displacement method mean (standard error)	1·04[a]	0·11[a] (0·05, 0·05)[c]			14·03[a] (6·06)[d]	37·94[a] (16·17)[d]	

ρ_s*, seed density (g/cm^3); V_c, critical velocity (m/s) calculated using quartz-equivalent diameter; FV_l, flume measured low friction bed transport velocity (m/s); FV_g, flume measured gravel bed transport velocity (m/s); V_{oi}, inertial settling ('Impact') law (cm/s); V_{ow}, Wu and Wang settling velocity (cm/s); V_{op}, pool measured settling velocity (cm/s).
[a] Significant differences at the $p < 0{\cdot}0001$ level between prolate spheroid and water displacement-based estimations.
[b] Significant differences at the $p < 0{\cdot}0001$ level between flume and pool empirical observations and equation-based estimates.
[c] Standard error of the estimate of V_c compared to both the FV_l and FV_g observations.
[d] Standard error of the estimate of V_{oi} and V_{ow} compared with the V_{op} observations.

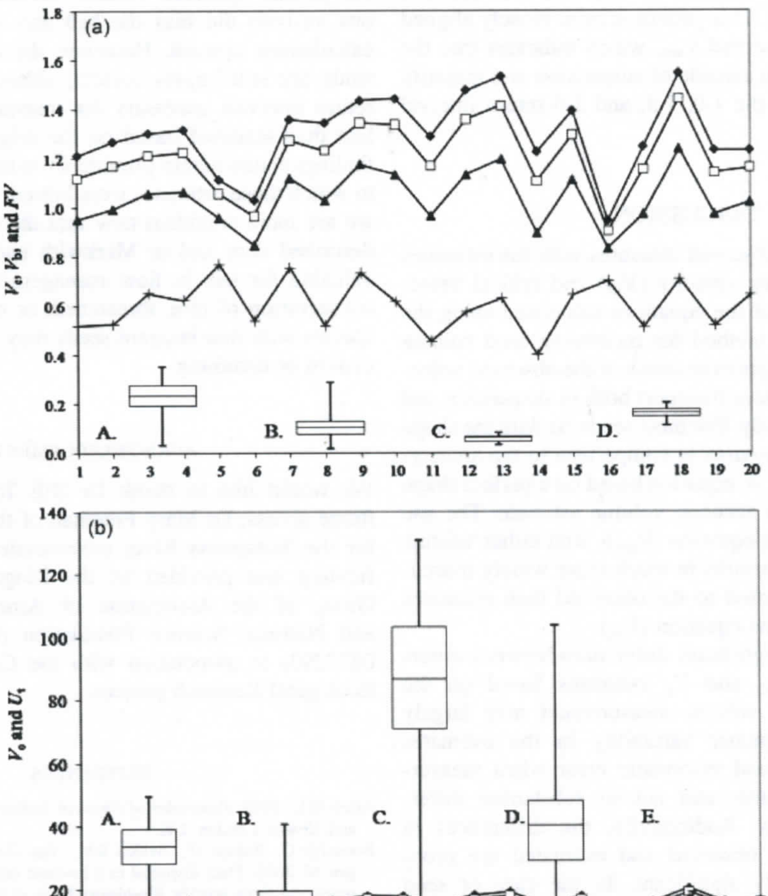

Figure 1. Modeled stream reach velocities for the 0·5 (+), 1·0 (▲), 1·5 (□), and 2·0 (◆) return intervals graphed with calculated and observed seed parameter box and whisker plots. (a) Includes modeled bed velocity (V_b) compared to seed critical velocity (V_c) estimated and observed using, (A) the prolate spheroid method, (B) the water displacement method, (C) low friction flume (FV_l), and (D) gravel bed flume (FV_g). (b) Includes modeled shear velocity (U_τ) compared with seed settling velocity estimated and observed using, (A) the inertial settling velocity equation (V_{oi}) based on prolate spheroid density, (B) the inertial settling velocity (V_{oi}) equation based on water displacement density, (C) Wu and Wang (V_{ow}) equation based on prolate spheroid density, (D) Wu and Wang (V_{ow}) equation based on water displacement density, and (E) the observed settling velocity (V_{op}) of a seed falling through 1·5 m of water.

also significantly different from each other (Table I). Observed V_{op} values are significantly less than either V_{oi} calculation or either V_{ow} calculation. The V_{oi} calculated using water displacement method has a mean closest to the observed V_{op}. There is a major outlier on the upper end of the V_{oi} estimates based on the water displacement method (38·46 cm/s). The next highest value is 23·68 cm/s. Removing that outlier reduces the mean to 13·56 cm/s, however the estimate remains significantly different from the observed ($p < 0{\cdot}001$).

The majority of the seed V_{oi} estimates based on the prolate spheroid method are greater than the shear velocities (U_{τ}) of all four return interval flows at all cross sections (Figure 1b). This is also true for both estimation methods using the V_{ow} equation. On the other hand, a majority of the V_{oi} estimates based on the water displacement method are less than U_{τ} at a large proportion of cross sections at both the 1·5 and 2·0 return interval flows. This pattern is most closely aligned with that of the observed V_{op}, which indicates that the majority of seeds are capable of suspension at a majority of cross sections at the 1·0, 1·5, and 2·0 return interval flows.

DISCUSSION

Comparison of the observed measures with the estimates of the inertial settling velocity (V_{oi}) and critical velocity (V_c) indicates that the equations calculated using the water displacement method for measuring seed volume provide reasonable approximations of the observed velocities required to achieve transport both in suspension and on the bed, respectively. For most seeds, as with the shape variability of *H. coronaria* in comparison to the archetypal prolate spheroid, an equation based on a perfect shape does not provide an accurate volume estimate. The use of the Wu and Wang equation (V_{ow}), with either volume calculation method, results in much more widely inaccurate estimates compared to the observed than estimates from the 'impact' law equation (V_{oi}).

The statistically significant differences between observations and the V_{oi} and V_c estimates based on the water displacement volume measurement may largely be the result of greater variability in the estimates caused by random and systematic error when measuring mass and volume, and not to substantial differences in the means. Additionally, the differences in the means between observed and estimated are probably not biologically significant. In the case of seed transport, biological significance is related to the frequency at which the average seed can be moved among populations or to new habitat for colonization. Both observed and estimated parameters indicated that seeds move on the bed with flows well below the 0·5 year return interval, and thus substantial seed movement every year can be concluded from either method. This conclusion is similarly appropriate for comparison of the observed settling velocity and the water displacement volume based inertial settling velocity estimates. The observed V_{op} values indicate a return interval of 1·0–1·5 years is sufficient to generate flows capable of suspending the average seed, while the V_{oi} estimates indicate 1·5–2·0 year return intervals. In the case of a relatively long-lived perennial like *H. coronaria* a return interval difference of 0·5–1·0 years is probably not significant to microevolution or population dynamics. Perhaps such a statistical difference would be more biologically significant for species with an annual lifecycle and very unstable populations, but even under those circumstances the estimation methods described herein may be appropriate.

This study confirms the assumptions of Markwith and Leigh (2008) that the application of sediment transport equations to analyze non-buoyant seed transport is a valid method for examining the temporal and spatial characteristics of subaqueous hydrochory. The use of the prolate spheroid volume calculation in the previous analysis did bias the bed and suspended transport calculations upward. However, the conclusions of that study are still largely correct, although the actual flow return intervals necessary for transport may be slightly less than assumed based on the original estimates. The findings found herein provide an indication of the degree to which those estimates were biased. Given these results, we are more confident now that the estimation methods described here and in Markwith and Leigh (2008) are valuable for use in flow management scenarios where conservation of rare, threatened, or otherwise important species with non-buoyant seeds may be affected by regulation or damming.

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