FEATURE ARTICLE

Windows of opportunity: thresholds to mangrove seedling establishment on tidal flats

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ABSTRACT: Physical processes limiting colonization of bare tidal flats by pioneer mangrove species have commonly been described but not yet quantified. Understanding thresholds to early seedling establishment is critical for successful restoration and management of mangrove forests. We determined how seedling establishment of *Avicennia alba* Bl. is affected by the combination of increasing hydrodynamic forces and sediment dynamics. As the buoyant propagules of *A. alba* are dispersed by water, early establishment on bare tidal flats requires propagules to quickly anchor to stay in place. Flume studies and field observations showed that 3 thresholds have to be passed until the seedling is successfully established: (1) stranded propagules need an inundation-free period to rapidly develop roots that are long enough to withstand displacement by flooding, (2) roots need to become long enough to withstand seedling dislodgement by hydrodynamic forces from waves and currents, with the required root length being proportional to the force that needs to be resisted, (3) even longer roots are needed to survive high energy events that cause sheet erosion and can thereby induce seedling dislodgement. This sequence of thresholds implies that establishment of the pioneer mangrove species *A. alba* requires a suitable window of opportunity to pass all thresholds and underlines the importance of rapid root expansion as a crucial pioneer trait for the species.

KEY WORDS: *Avicennia* · Colonization · Flume · Pioneer · Mangrove restoration · Seedling establishment · Succession · Threshold

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INTRODUCTION

Mangroves are rapidly declining worldwide, with the largest total loss (1900 million hectares) occurring in Asia from 1980 to 2005 (Duke et al. 2007, FAO 2007). Once destroyed, restoration of mangroves along the coast is difficult (Erftemeijer & Lewis 2000, Alongi 2002) unless conditions are favorable (Field 1998, Lugo 1998). Similar problems in restoration have been reported for other coastal vegetation such
as salt marshes (e.g. Wolters et al. 2005) and seagrass beds (e.g. Van Katwijk et al. 2009). The latter implies that there can be thresholds for seedling establishment on bare tidal flats that must be surpassed for successful colonization. If these thresholds are related to disturbance varying in space and time, seedling establishment requires windows of opportunity where disturbance is low or absent (Romme et al. 1998, Proisy et al. 2009). There is a general lack of mechanistic understanding of processes that cause thresholds to seedling establishment of coastal pioneer vegetation (Bouma et al. 2009a, Friess et al. 2011). Generating a mechanistic understanding of the thresholds that limit colonization of bare tidal flats by mangroves is a key to identifying boundary conditions that offer the window of opportunity for mangrove establishment. This is of critical importance for mangrove management, e.g. as a decision tool to determine where proactive versus passive restoration should be attempted.

Avicennia is the most widespread genus of mangrove pioneer trees, colonizing bare tidal flats of tropical regions around the world (see Osborne & Berjak 1997 for A. marina in Africa; Lee et al. 1996, Panapitukkul et al. 1998 for A. alba in SE Asia; Mark hand et al. 2004, Proisy et al. 2009 for A. germinans in South America; Clarke 1993 for A. marina in Australia). When conditions are favorable, instantaneous colonization of tens of hectares by Avicennia can take place in a few days as reported for migrating mud banks in South America (Proisy et al. 2009). Avicennia seedlings are well adapted to the harsh intertidal environment where flooding and anoxic soils limit plant growth (Clarke 1993, Osborne & Berjak 1997), and these species produce relatively large numbers of cryptoviviparous propagules (i.e. only partly germinating while still on the tree) that are distributed by the tide (Panapitukkul et al. 1998) and establish rapidly after stranding (Osborne & Berjak 1997). Although the embryo is always developmentally active, recalcitrancy (hence, moisture) is likely to control germination after release (Osborne & Berjak 1997, Le Tam et al. 2004). Up to 6 additional root primordia remain suppressed during the first stranding, enabling Avicennia propagules to anchor in a second or third stranding (Osborne & Berjak 1997).

Earlier studies on mangrove establishment mostly focused on phenology of the parent tree, buoyancy times of propagules or survival of seedlings in the sapling stage that were already successfully established (Di Nitto et al. 2008, Krauss et al. 2008). Thampanya et al. (2002) demonstrated indirectly that colonizers such as Avicennia alba and Sonneratia alba have greater survival rates at exposed sites with high hydrodynamic energy than Rhizophora sp. However, still little is known about how hydrodynamic and geomorphological processes may hamper the initial establishment of stranded Avicennia propagules.

In this study we quantify the thresholds to initial seedling establishment by a combination of flume experiments and field measurements. For different developmental phases of the very young seedling, we determined which factor was most critical for survival and how this factor changed with root development.

**MATERIALS AND METHODS**

**Seedling growth conditions**

Propagules of Avicennia alba were collected from Singapore mangroves and brought to the Netherlands within 48 h in a moist container. They were cultivated immediately in a climate room, which was held at 30°C and provided an average of 12 h d⁻¹ of 550 μmol m⁻² s⁻¹ photosynthetically active radiation (PAR), on arrival. The experiment was completed 13 d after receipt and immediate planting. Propagules were laid on top of marine sand in individual PVC pipes with dimensions of 150 mm height and 120 mm diameter, which had open bottoms and were lined with polyethylene bags. The sand was kept waterlogged throughout the experiment. This setup simulated natural stranding on the tidal flat, free from tidal inundation. The pot design allowed us to measure in a flume both the hydrodynamic stress and sediment disturbance that seedlings could withstand before getting dislodged (see next section for details). Seedcoats were already shed at the time of planting, and any root primordia were <5 mm in length. For simplification, hereafter all propagules showing their first roots are called seedlings. From Days 5 to 13 after planting, 10 pots were randomly selected each day and subjected to the flume experiment. Root growth was measured after the flume experiments.

**Flume experiments on seedling dislodgment**

The flume consisted of a 17.5 m long and 0.6 m wide oval racetrack that could produce currents and waves (Bouma et al. 2009b). A double bottom in the test section allowed the cut PVC pipes filled with sediment to be inserted flush with the flume bed, leaving only the seedling exposed (Fig. 1). No significant scouring was observed. Flume water depth was
maintained at 32 cm. A constant current of 3.5 cm s\(^{-1}\)
was applied with a conveyor belt, and wave energy
was varied by adjusting the wave paddle. Maximum
bed shear stress was calculated from pressure sensor
(GE Druck PTX1830) measurements, as a measure
for the hydrodynamic forcing on the seedling at the
bottom of the flume. The experimental conditions
allowed us to apply Jonsson’s (1966) formula to cal-
culate maximum bed shear stress due to waves.
Additional bed shear stresses due to the slow current
in the flume were quantified by calculating the
apparent roughness height for the flume bottom for
waves propagating in the same direction as the
current (van Rijn 1993). Time-averaged total bed
shear stress was subsequently calculated by adding
both components. A reduction factor for the current-
induced bed shear stress due to the presence of the
waves was applied (van Rijn 2008). Maximum bed
shear stress of waves and current have been derived
by adding the total time-averaged bed shear stress
and maximum shear stress under waves, as both
have the same direction (Soulsby 1997). Equations
used are explained in Appendix 1.

Three different tests were carried out in the flume.
(1) The pots were slowly submerged to test whether
the seedlings would float up. (2) If the seedlings
stayed in place, bed shear stress was increased from
0.17 to 0.52 N m\(^{-2}\) in a maximum of 13 increments
with each increment lasting approximately 2 min. (3)
For seedlings that resisted the maximum bottom
shear stress of 0.52 N m\(^{-2}\) in Test 2, we determined
their critical vertical erosion, which was defined as
the amount of sediment that needed to be removed
from around a seedling in order to
dislodge it. The critical erosion at dis-
lodgement was determined by raising
the sediment incrementally by plac-
ing PVC discs of 3 mm thickness
underneath the pipe. Sediment at the
top of the PVC pipe was gently
removed by hand to keep the sedi-
ment level flush with the flume bot-
tom. After each step-wise sediment
removal, seedlings were exposed to a
maximum bed shear stress of 0.27 N
m\(^{-2}\) (i.e. wave height of 6 cm). This
protocol was repeated until dis-
lodgement occurred. After dislodge-
ment, root length of the longest,
last dislodged root was measured. We
observed no root snapping during
this experiment that would confound
root length measurements.

**Seedling dislodgement with drag scale**

To corroborate the flume experiments, we con-
ducted field measurements to determine both the
minimum root length that could be observed on
established seedlings in the field and the forces
needed to remove recently anchored seedlings from
the mudflat. *Avicennia* propagules/seedlings were
randomly selected within survey quadrats at 3 con-
trasting locations (along inundation gradient) in the
Mandai mangrove forest in Singapore. A spring scale
with 20% tare error and 1 g reading error (Pesola
Medio-Line 40300 with drag pointer) was clipped to
the top of each propagule/seedling and carefully
pulled upward until dislodgement, and the force
needed to dislodge the seedlings was read directly
from the scale. If the propagule/seedling was not
anchored yet, i.e. there was no root penetration into
the substrate, no value was recorded. The frictional
force of the attached drag pointer (40 g 0.4 N, see
www.pesola.com) was accounted for in the analysis.
The weight of the seedling (1 to 3 g ~0.01 to 0.03 N)
was deducted from the pulling force. Maximum root
length was measured for all dislodged seedlings.

As we did not find seedlings with root lengths
below 2.5 cm, we planted small propagules in pots
with waterlogged mangrove mud. After 2 to 3 d
of establishment, the same pulling test was carried
out on these small seedlings. Snapping of roots
did not occur due to the soft substrate and the short
roots.
RESULTS

Seedling root growth

The first root primordia were visible 2 d after simulated stranding, and on the third day the maximum root length was 1 cm. At least 75% of all propagules had developed visible roots by Day 4. On Day 6, the first seedlings were found to be erect due to extension of the hypocotyl. On Day 8, 24.5% of all seedlings had expanded cotyledons. Root length increased linearly from Days 5 to 13 after planting (Fig. 2). Seedlings developed 1 to 5 roots over the course of the experiments.

Flume experiments on seedling dislodgement

On average, a minimum root length of 2 cm was required to prevent the buoyant propagule from floating up when inundated, without hydrodynamic force from waves or currents (Fig. 3). Until the last day (Day 13), seedlings showed buoyancy after dislodgment. Seedlings with a maximum root length between 2 and 4 cm were sensitive to dislodgment due to wave action. The bed shear stress that caused seedling dislodgment was linearly related to the length of the longest root of the seedling (Fig. 3). Above a maximum root length of 4 cm (Fig. 3), seedlings could no longer be dislodged by the maximum bottom shear stress that we could impose in the flume, which was determined by water height and wave paddle design. In our study, this root length was reached on average after 8 d (Fig. 2). Critical erosion at dislodgement was linearly correlated with maximum root length (Fig. 4); 4 cm of the longest root

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Fig. 2. Avicennia alba. Maximum root length ($R_{\text{max}}$; cm) as a function of time since stranding of the propagule ($T$; d). Root growth was measured on a maximum of 10 harvested seedlings per day ($N = 76$, nongerminated propagules were excluded). The maximum root length could be characterized by the linear regression: $R_{\text{max}} = 0.75 \times T - 1.62$ ($R^2 = 0.49$)

Fig. 3. Avicennia alba. The hydrodynamic force expressed as bed shear stress ($\tau_b$; N m$^{-2}$) that can be resisted before seedlings (fixed seedlings: $N = 28$, dislodged seedlings: $N = 42$) with maximum root length ($R_{\text{max}}$, cm) were dislodged. Seedlings with $\leq 2$ cm roots would float up when flooded, even in the absence of any waves or current. The bed shear stress experienced by seedlings at the flume bottom at the moment of dislodgment increased linearly with maximum root length: $\tau_b = 0.1071 \times R_{\text{max}} - 0.0113$ ($R^2 = 0.75$). Once the maximum root length exceeded 4 cm, all seedlings were stable and could resist the highest level of bed shear stress applied in the flume

Fig. 4. Avicennia alba. The critical vertical erosion ($E_{\text{crit}}$; cm) that needs to be surpassed to dislodge seedlings ($N = 15$) of different root lengths ($R_{\text{max}}$ cm). For a constant bed shear stress of 0.27 N m$^{-2}$, the maximum root length is linearly correlated with the critical vertical erosion that was mimicked in the flume: $E_{\text{crit}} = 0.93 \times R_{\text{max}} + 3.79$ ($R^2 = 0.79$)

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Seedling dislodgement with drag scale

Based on the flume results, which demonstrated the important role that roots have in seedling survival (Figs. 3 & 4), we measured the minimal root length that can be observed on established seedlings in the field and how root length affects the (vertical) force seedlings can resist before uprooting. All naturally established seedlings were found to have at least 1 root with a length greater than 2.5 cm (Fig. 5). For
both experimentally planted and in situ seedlings, the force needed to vertically pull a seedling (root anchorage plus seedling weight) out of the soil increased exponentially with maximum root length (Fig. 5). Thus, the length of the longest root proved to be a good proxy for anchorage strength, both in the flume (Figs. 3 & 4) and in the drag scale experiment (Fig. 5). A small increase in root length leads to a large increase in stability during the earliest seedling stage (i.e. root <5 cm). The exponential increase of the drag scale field data compared with the linear relationship obtained in the flume might be explained by increased soil compaction with depth for the deeper rooting seedlings in the field and presence of fine roots for seedlings with approximately >5 cm maximum root length. Resolving this requires further studies in the future.

**DISCUSSION**

**Thresholds to early seedling establishment and windows of opportunity**

Despite the growing concern for global mangrove loss and the interest in mangrove dynamics and establishment (Krauss et al. 2008), similar to those for salt marshes and seagrass beds (Bouma et al. 2009a), a general understanding of the mechanistic processes underlying the apparent thresholds to early establishment of pioneer species is lacking (Di Nitto et al. 2008). To our knowledge the present study is the first to provide a mechanistic insight on how disturbance by hydrodynamic forces and associated sediment dynamics defines thresholds to Avicennia colonization on a tidal flat. Based on our results, we distinguish 3 thresholds during seedling establishment (Fig. 6). First, anchorage of A. alba propagules requires a minimum period during which it is free from inundation after stranding. Second, root growth has to surpass a minimum length to withstand disturbance by hydrodynamic forces by waves and currents imposed on the seedlings. Third, root length needs to be sufficient to resist disturbances from removal of sediment around the seedling, which can be caused by sediment mixing and/or sheet erosion (Fig. 6). The latter is important for bare mudflat colonization, as previous research has demonstrated that physical mixing of the upper sediment layer on mudflats is substantial and the mixing depth decreases in a landward direction (e.g. 4 to 30 cm over a 100 d period for a Brazilian mangrove, Smoak & Patchineelam 1999).

Less disturbance can be expected inside the forest due to root structures attenuating hydrodynamic energy. By using non-cohesive sediments in the flume we show that exceeding the critical bed shear stress for sediment movement (cf. Soulsby 1997) without dislodging the propagule is possible, hence supporting the existence of the third threshold in which the seedling gets excavated.

**Fig. 5. Avicennia alba.** The critical vertical drag force needed for seedling (field: N = 26, planted: N = 24) dislodgement (\(F_{\text{crit}}\); N) is correlated exponentially to the maximum root length (\(R_{\text{max}}\); cm): \(F_{\text{crit}} = 0.2877e^{0.3196R_{\text{max}}}\) \((R^2 = 0.73)\). Error bars represent the tare error of 20% of the spring scale. Especially for small seedlings with maximum root lengths of <5 cm, a small increase in root length is important to enhance anchorage. As there were no field seedlings with a maximum root length <3 cm, we planted seedlings in pots filled with mangrove mud (‘experiment’)

**Fig. 6. Avicennia alba.** Schematic representation of the 3 thresholds that need to be reached during establishment of an Avicennia seedling. Magnitude of disturbance increases from left to right. After the seed coat is shed the propagule starts to put out its roots to anchor in the sediment. (1) The propagule first has to acquire a minimum root length during an inundation-free period to resist against floating up during tidal inundation. (2) Thereafter, roots need to be long enough to resist forces by wave and currents. (3) After the roots penetrate several centimeters into the sediment, only mixing or erosion of the upper sediment layer can still lead to dislodgement
Although the mechanisms of early seedling establishment will likely be generally valid, the actual threshold values may also vary depending on local conditions. For example, root extension rate (Fig. 2) can be expected to vary with abiotic conditions such as salinity and temperature (Krauss et al. 2008). The minimal root length needed to withstand floating immediately following stranding, and subsequently to withstand hydrodynamic drag forces (which was in our case 4 cm), will be variable depending on factors such as sediment composition and the local wave climate. For example, breaking waves at lower water levels may impose higher forces in the field with longer durations of exposure than we mimicked in the flume. In that case, longer roots would be needed to anchor the seedling. However, cohesive muddy sediments may give more support to the roots than the loose sand used in present experiments, in which case shorter roots could be sufficient.

Being amongst the most successful mangrove colonizers, *Avicennia* appears to be well adapted to establish on dynamic bare mudflats. That is, *Avicennia* is able to anchor rapidly, resist hydrodynamic forces from waves and currents within a few days, and then resist sediment movements of the upper sediment layer. The presence of thresholds (i.e. a seedling either has sufficient time to anchor or is dislodged), provides an explanation for observations of colonizers, *Avicennia* cohorts (e.g. Proisy et al. 2009), which presumably occurs whenever windows of opportunity open up and propagules are available. Such conditions could occur at neap tides during the fruiting season. Mass establishment of *Avicennia* may be reflected in even-aged stands of *Avicennia* on the tidal flat. The mudflat remains bare in front of more mature mangrove stands where thresholds can not be surpassed. The experiments underline the importance of coastal hydrodynamics and resulting sediment dynamics in mangrove regeneration and colonization processes (Fromard et al. 2004). Concurrence of windows of opportunity (e.g. depending on tides and weather) and propagule availability (i.e. fruiting seasons) are likely to be important for colonization success and ecosystem stability.

**Implications for application**

The demonstration of thresholds for mangrove seedling establishment implies that gradual change of the drivers (hydrodynamics, sediment dynamics) may cause an abrupt shift in the success of mangrove seedling establishment. Anthropogenic processes that change these drivers (e.g. coastal infrastructure works or increased boat traffic) could affect the boundary conditions for seedling establishment on a mudflat. The present study indicates that the threshold dynamics should be considered when impacts of anthropogenic influences or global change processes are assessed.

Where active reforestation is likely to be limited by disturbance, e.g. in fringing mangroves, consideration of the threshold dynamics can help to increase restoration success. A site is only suitable if (1) the inundation frequency is within acceptable physiological limits for each species (Lewis 2005), (2) the phase of the tidal cycle regularly allows propagules to strand and anchor during windows of opportunity, and (3) the sediment is firm enough to minimize mixing and erosion. As emphasized by Lewis (2005), planting mangroves on any convenient bare mudflat is not wise, as ‘there is a reason why mangroves are not already there (...) find out why’. The mechanistic approach we used to identify threshold dynamics for seedling establishment offers an important tool in this process.

**Acknowledgements.** Research was conducted under Singapore NParks permit number NP/RP936-1. We gratefully acknowledge the NIOO-CEME for the use of the flume and mesocosm facilities and D. Galli for supporting field work in Singapore. Funding was provided by the Singapore-Delft Water Alliance Marine 3 programme, grant number R-264-001-024-414, National University of Singapore.

**LITERATURE CITED**

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The flume used for the experiments described in this paper consisted of a 17.5 m long and 0.6 m wide oval racetrack that can produce currents and waves simultaneously. During this study the water depth was maintained at 32 cm, a constant current of 3.5 cm s\(^{-1}\) was applied with a conveyor belt and wave heights were varied by adjusting the frequency of the wave paddle. Maximum bed shear stress was calculated from pressure sensor measurements (sampled at 25 Hz). This pressure signal was first translated in water depths. From these water level fluctuations, wave heights and periods could be derived by simple signal analysis. The calculation of maximum bed shear stresses from the combined action of these waves and the current are explained by summarizing the equations applied. First is an explanation of the calculation of shear stresses under waves using linear wave theory, which was valid in our experiments. Subsequently, shear stresses under a steady current are calculated and finally both components are combined.

### Bed shear stresses under waves

As stated, wave heights (\(H\)), water depths (\(h\)) and wave periods (\(T\)) are predefined in the flume. We show step by step how to calculate the bed shear stress due to waves from these basic parameters.

**Wavelength.** According to linear wave theory, wavelengths (\(L\)) can be calculated as follows from the dispersion relationship:

\[
\omega^2 = gk \tanh kh \tag{A1}
\]

where \(\omega\) represents the angular frequency (\(2\pi/T\)), \(g\) the gravitational acceleration constant and \(k\) the wave number (\(2\pi/L\)). This dispersion relation can be rewritten as:

\[
L = L_0 \tanh \frac{2\pi h}{L} \quad \text{with} \quad L_0 = \frac{gT^2}{2\pi} \tag{A2}
\]

This formula cannot be solved directly and needs an iterative solution procedure. In order to calculate \(L\), \(L_0\) was used as a first estimate of the wavelength; hence \(L\) on the right-hand side of the equation can be substituted by \(L_0\). A second estimate of the wavelength (i.e. \(L_1\)) can be calculated. This value can be substituted into the right-hand side of the equation again (note not to substitute \(L_0\) but only \(L_1\)) to calculate another new value of the wavelength (\(L_2\)). This procedure can then be repeated until subsequent calculations of the wavelength show a difference of <1%.

The non-linearity of observed waves can be expressed by the Ursell number (\(U_r\)): \(U_r = \frac{HL^2}{h^3}\) \(\tag{A3}\)

In general, when \(U_r > 15\), non-linear wave theory is assumed to be more reliable. For all of our wave conditions, the Ursell number was below 15, so linear wave theory could be applied.

**Orbital velocity.** Orbital flow velocities of water particles due to wave motion can be calculated through the derivative of the velocity potential (\(\phi\)), which for linear waves is represented by:

\[
\phi(x, z, t) = \frac{\omega H \cosh k(z + h) \cos(\omega t - kx)}{2k \sinh kh} \tag{A4}
\]

where \(z\) represents the vertical distance to a reference plane (e.g. the average water level), \(x\) represents the horizontal distance, \(t\) is the time and \(h\) stands for the (average) water depth. Derivation of this formula for the \(x\)-direction (i.e. direction of propagation of the waves) results in the instantaneous horizontal velocity component in this direction (\(\hat{u}\)). This instantaneous horizontal velocity depends on the vertical position \(z\), the horizontal position \(x\) and the time \(t\):

\[
\hat{u}(x, z, t) = \frac{\partial \phi}{\partial x} \frac{\cosh k(z + h)}{\sinh kh} \sin(\omega t - kx) \tag{A5}
\]

Within the equation of the instantaneous velocity we distinguish between the harmonic component that consists of the final sine term in the equation above and the velocity amplitude (\(\hat{U}\)), which is constant over time at a certain position:

\[
\hat{U}_s = \frac{\omega H \cosh k(z + h)}{2 \sinh kh} \tag{A6}
\]

Near the bed (\(z = -h \to z + h = 0\)) this results in the following equation for the maximum horizontal orbital velocity (\(\hat{U}_s\)):

\[
\hat{u}_s = \frac{\omega H}{2 \sinh kh} \tag{A7}
\]

**Particle excursion.** Wave forces cause an orbital motion of the fluid particles and their excursion (amplitude) can be calculated by integrating the instantaneous velocity, as calculated above, over time. Assuming that both amplitudes in the \(x\) - and \(y\) -directions are negligible compared to \(x\) and \(z\) (small amplitude waves), this integration yields the following equation for the horizontal particle excursion (\(A\)) (van Rijn 2008):

\[
A = \frac{H \cosh k(z + h) \cos(\omega t - kx)}{2 \sinh kh} \tag{A8}
\]

Again, we can split this equation into, a harmonic part (\(\hat{A}\)) and a harmonic part. For the amplitude we find:

\[
\hat{A} = \frac{H \cosh k(z + h)}{2 \sinh kh} \tag{A9}
\]

The maximum horizontal excursion of the water particles at the bottom (\(\hat{A}_b\)) then reads:

\[
\hat{A}_b = \frac{H}{2 \sinh kh} \frac{\hat{U}_s}{\omega} \tag{A10}
\]

**Bottom friction.** The calculation of the wave-related friction coefficient (\(f_w\)) depends on the hydraulic regime that is present, whether it is a laminar, hydraulic smooth or hydraulic rough regime. Each of these regimes comes with its own conditions and method for calculating or approximating the wave-related friction coefficient (van Rijn 2008). The hydraulic regime is said to be laminar in cases where the following boundary condition applies (van Rijn 2008):

\[
\frac{H}{h} < 0.03 \tag{A11}
\]

**Bed shear stresses under waves.**

As stated, wave heights (\(H\)), water depths (\(h\)) and wave periods (\(T\)) are predefined in the flume. We show step by step how to calculate the bed shear stress due to waves from these basic parameters.
where \( V \) represents the kinematic viscosity, which is about \( 10^{-6} \text{ m}^2 \text{ s}^{-1} \) for seawater.

This condition was valid for all experimental conditions and in this case the wave-related friction coefficient can be calculated by Jonsson’s (1966) equation:

\[
f_w = 2 \left( \frac{U_b \delta}{v} \right)^{-0.5} \tag{A12}
\]

**Bed shear stress.** The maximum bed shear stress due to wave propagation (\( \tau_{b,w,\text{max}} \)) can subsequently be calculated by:

\[
\tau_{b,w,\text{max}} = 0.5 \rho f_w (U_b)^2 \tag{A13}
\]

where \( \rho \) represents density. Averaged over the time of half a wave cycle, Eq. (A13) becomes:

\[
\tau_{b,w} = 0.25 \rho f_w (U_b)^2 \tag{A14}
\]

Bed shear stresses always add up to zero if averaged over an entire wave cycle due to the oscillatory character of the waves.

**Bed shear stresses under flow**

For a constant flow through the flume (instead of waves), the time-averaged flow related bed shear stress (\( \tau_{b,c} \)) can be calculated by:

\[
\tau_{b,c} = 0.125 \rho f_c v^2 \tag{A15}
\]

where \( f_c \) represents the friction coefficient due to the current and \( v \) the depth-averaged flow velocity. The friction coefficient from water flow can be calculated from the typical Chézy coefficient (\( C \)) for the material and shape of the bottom of the flume:

\[
f_c = 8 \frac{g}{C} \tag{A16}
\]

The Chézy coefficient can be calculated from the roughness height \( k_s \) of the bed material, which is commonly known to be:

\[
C = 18 \log \left( \frac{12h}{k_s} \right) \tag{A17}
\]

For the smooth material (glass) of the sides and bottom of the flume, a \( k_s \) value of \( 2 \times 10^{-5} \text{ m} \) was assumed.

**Flow and waves**

When the waves and current coincide, the Chézy coefficient is calculated slightly differently:

\[
C = 18 \log \left( \frac{12h}{k_a} \right) \tag{A18}
\]

where \( k_a \) stands for the apparent roughness height of the bed material (van Rijn 2008). The apparent roughness height can be calculated by:

\[
k_a = k_s \exp \left( \frac{\gamma U_b}{\nu} \right) \text{ for } \frac{U_b}{\nu} \leq 5 \tag{A19}
\]

in which \( \gamma \) represents a coefficient accounting for the angle between the flow and the current. For waves following the current, a value of \( \gamma = 0.75 \) should be applied.

In this case, according to van Rijn (2008), the magnitude of the time-averaged total bed shear stress due to currents and waves together (\( \tau_{b,c,w} \)) can be calculated by:

\[
|\tau_{b,c,w}| = \alpha_r |\tau_{b,c}| + |\tau_{b,w}| \tag{A20}
\]

with \( \alpha_r \) being a reduction factor for the current-induced bed shear stress caused by the presence of the waves:

\[
\alpha_r = \frac{[\ln(30\delta/k_s)]^2}{[\ln(30\delta/k_s)]^2 + [\ln(30h/k_s)]^2} \tag{A21}
\]

with \( \delta \) representing the thickness of the bed boundary layer:

\[
\delta = 0.2 \delta_b (\delta_b/k_s)^{0.25} \tag{A22}
\]