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Research article

Simple rules based on pile slope are used in the self organization of sand pile formation by *Pheidole oxyops* ants

A. Tofilski[1] and F.L.W. Ratnieks[2]

[1] *Department of Pomology and Apiculture, Agricultural University, 29 Listopada 54, 31-425 Krakow, Poland, e-mail: rotofils@cyf-kr.edu.pl*
[2] *Laboratory of Apiculture and Social Insects, Department of Animal and Plant Sciences, Sheffield University, Western Bank, Sheffield S10 2TN, United Kingdom, e-mail: F.Ratnieks@Sheffield.ac.uk*

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Abstract. We tested the hypothesis that slope influences where worker ants deposit excavated soil on piles near the nest entrance. We predicted that ants will deposit their load near the top of a pile where the slope changes from upward to downward, to prevent material rolling back towards the entrance. We tested this hypothesis by studying five natural colonies of *Pheidole oxyops* ants at a field site at São Simão, Brazil. At this site, each colony was dumping sandy soil excavated from its underground nest in a crescent-shaped pile c. 13 cm from and perpendicular to the nest entrance. Each nest was given an experimental sand pile of symmetrical curved cross section on a plywood platform that could be tilted 15 degrees up or down. From videos, the locations where individual ants dumped their soil loads were measured in relation to the inner (position = 0) and outer (position = 1) edges of the pile. When the platform was tilted down the ants deposited their loads significantly closer to the inner edge (0.458 ± 0.007) than when not tilted (0.530 ± 0.006). When the platform was tilted up the ants deposited their loads significantly further from the inner edge (0.626 ± 0.006) than when not tilted (0.522 ± 0.006). These results support the hypothesis that ants use pile slope in deciding where to dump their load. A similar rule is probably used in other ant species that place excavated soil in steep piles near the nest entrance.

Keywords: Sand pile, nest excavation, self-organization, *Pheidole oxyops.*

Introduction

The natural world is full of spatial patterns and shapes. A key question in the study of these patterns is to determine how they are generated (Ball, 1999). For example, how do sand dunes and snowflakes assume their characteristic shapes? Pattern and shape are of particular importance in biology. Some of the best-known examples arise from the building activities of insect societies. Most obviously, many social insects build elaborate nests to an overall design often with characteristic smaller structures such as the hexagonal cells of honeybees and Vespidae wasps (Frisch, 1974). These nest structures can be built by the combined activities of many individual insects, each following a simple set of rules (Theraulaz and Bonabeau, 1995). Social insects also form spatial patterns outside their nest. Many ant and termite species form trail networks leading from the nest entrance into the surrounding environment (Wilson, 1971), and many ground-nesting ants construct piles of excavated soil near the nest entrance (Wheeler, 1910; Halley et al., 2005).

In many habitats, and especially in warmer climates with many ground-nesting species, ant soil dumps are abundant and diverse. Some species build circular piles or "craters" around the entrance, whereas in others the pile is to one side and may be kidney or crescent shaped, often forming a ramp or wall. There is also diversity in the height of the pile from almost flat to steeply sloping, often to the point that the outer slope is unstable and subject to repeated small landslides as more soil is dumped (Tofilski and Ratnieks, 2005).

Colonies of the Brazilian ant, *Dorymyrmex* sp., build circular piles of excavated soil around their nest entrances. The outer slope is steep and unstable. Workers carrying soil preferentially release their loads near the outer edge of the top of the pile (Tofilski and Ratnieks, 2005). Most particles remain where they were placed (77.5 %), and almost all that roll do so on the outer slope away from the entrance. Very few (0.1 %) soil particles roll back on the inner slope towards the entrance. As a result, although piles grow both taller and wider in diameter as more soil is dumped, the inner surface of the pile remains at an angle that is too shallow for it to collapse back into the entrance hole. If this were to happen it would waste a great deal of work (Franks et al., 2004).

According to Theraulaz et al. (2003) the main mechanisms used by social insects to build sand piles and other spatial patterns are templates, stigmergy and self-organization or combinations of those. If ants leave the nest entrance in random directions and dump their loads at distances randomly taken from a Gaussian normal distribution this will result in a circular crater with a relatively uniform height (Sumpter, 2006). The use of this distribution as a template was suggested as the mechanism of sand pile formation in *Messor barbatus* ants (Chretien, 1969 cited by Theraulaz et al., 2003). Alternatively, sand piles of this shape could be formed via self organization (Camazine et al., 2001) if individual ants carrying soil follow a simple rule, by releasing their load when the angle of the pile changes from sloping up, to flat or sloping down (Tofilski and Ratnieks, 2005). This is a form of stigmergy (Grassé, 1959; Darchen, 1962) where modification of the structure under construction affects subsequent behaviour by other colony members. In other words there is feedback. In principle, individual ants could collectively build a soil pile to a defined shape using only local information about the pile, such as its slope, without central control or global knowledge about the shape of the whole pile. If this is the case then the mechanism relies on self-organization (Camazine et al., 2001). If ants use self-organization that involves assessing the slope of their colony's pile and depositing their loads near the top (flat) of the outer edge (sloping down) of the pile, then we predict that individuals should alter the distance at which they deposit their loads if the soil pile is experimentally tilted. On the other hand, if individual ants use only a template (e.g., have only a preferred distance at which to dump their soil), then load deposition should be independent of the slope conditions (Sumpter, 2006) and experimentally altering the slope of the pile should not affect deposition locations.

Here we test the self-organization hypothesis (Tofilski and Ratnieks, 2005) in an experimental study of another Brazilian ant, *Pheidole oxyops.* By replacing the colony's natural soil pile with an experimental pile mounted on a wooden platform that could be angled up or down, we show that the angle of the pile strongly affects where individual ants release their load in the predicted way. When the platform was angled down dumping occurred closer to the entrance, and vice versa.

Materials and methods

We studied *Pheidole oxyops* colonies living in sandy soil in the farmyard of Fazenda Aretuzinha, near the town of São Simão in São Paulo State, Brazil, in January and February 2005. This species builds a slightly curved (crescent-shaped) pile of excavated sand on one side of and perpendicular to the nest entrance. Workers transporting soil particles were approximately 4–5 mm in body length and their loads were approximately 1–2 mm in diameter. The distance between the edge of the nest entrance to the tops of the natural sand piles of the five study colonies was 127 ± 14 mm (mean ± SE), and the mean length (from one end to the other) and width (from inner to outer edge) were 188 ± 14 mm and 45 ± 4 mm, respectively. The distances from the inner and outer edges to the tops of the sand piles were 32 ± 2 mm and 12 ± 3 mm respectively. The inner slopes of the piles were relatively gentle and not subject to collapse, while the outer slopes were steep and unstable (Fig. 1a). As a result, this species was suitable to test the hypothesis of Tofilski and Ratnieks (2005) even though the piles were not circular as in *Dorymyrmex* sp.

In each colony, the original pile was removed, placed on a flat plywood platform (150 mm × 150 mm), and shaped into an experimental pile of standard size and cross section by dragging a rectangular piece of cardboard with a cut away portion across the pile. The experimental pile was 150 mm long and 100 mm from the nest entrance with the two ends equidistant to the entrance (Fig. 1c) similar to natural piles. In cross section the pile was a segment of a circle 30 mm in diameter, and was 10 mm high and 45 mm wide (Fig. 1b, 4). As such, the experimental pile was more symmetrical than natural piles because the inner and outer slopes were identical, and was less steeply sloping especially on the outer slope. This difference was deliberate. We needed a shallow slope to prevent the pile from collapsing when it was tilted up or down, and a symmetrical cross section so that the same distance from the apex of the pile would mean the same angle on both the inner and outer slopes. In addition, because natural sand piles have an abrupt change in slope angle at the apex (the start of the outer slope) tilting a natural sand pile by 15 degrees would have resulted either in no change or in only a small change of the position of the apex. This would have resulted in zero or small changes in the predicted dumping locations.

The platform supporting the experimental pile was hinged with tape to a second piece of plywood lying between the platform and the nest entrance. This allowed the platform to be tilted without causing cracks or bumps to form in the path taken by the ants from the entrance to the pile, which might have interfered with soil dumping.

During the experiment, soil dumping was video recorded (frame size 720 × 576 pixels, 25 frames per second) when the sand pile was in three positions: level (platform at 0 degrees), tilted up (+ 15 degrees), and tilted down (– 15 degrees, Fig. 1b). The video recorder was tilted the same angle as the platform so that its optical axis was always perpendicular to the platform. There were two sequences of recording: level, up, level, down; level, down, level, up. Each colony was recorded for 60 minutes continuously to give four 15-minute intervals. Video was downloaded onto a computer hard drive and analysed using VideoPoint software (Lenox Softworks). Frame by frame analysis allowed us to determine both the time and place each load was deposited. We measured these positions on a scale from 0 (inner edge of pile) to 1 (outer edge of pile). Not all dumping occurred on the pile. Positions between the nest entrance and the inner edge have negative values, and positions further than the outer edge have values above one.

When the platform is level, the apex of the pile is in position 0.5. When the platform is up (+ 15 degrees) the apex is further from the inner edge at position 0.62, and is at 0.38 when the platform is down (– 15 degrees) (Fig. 4, Appendix). Thus, the apex moves 0.12 in position when the platform is tilted. Therefore, we predicted that the mean dumping location should also move 0.12 when the platform was tilted if ants only use the angle of slope to influence their dumping position.

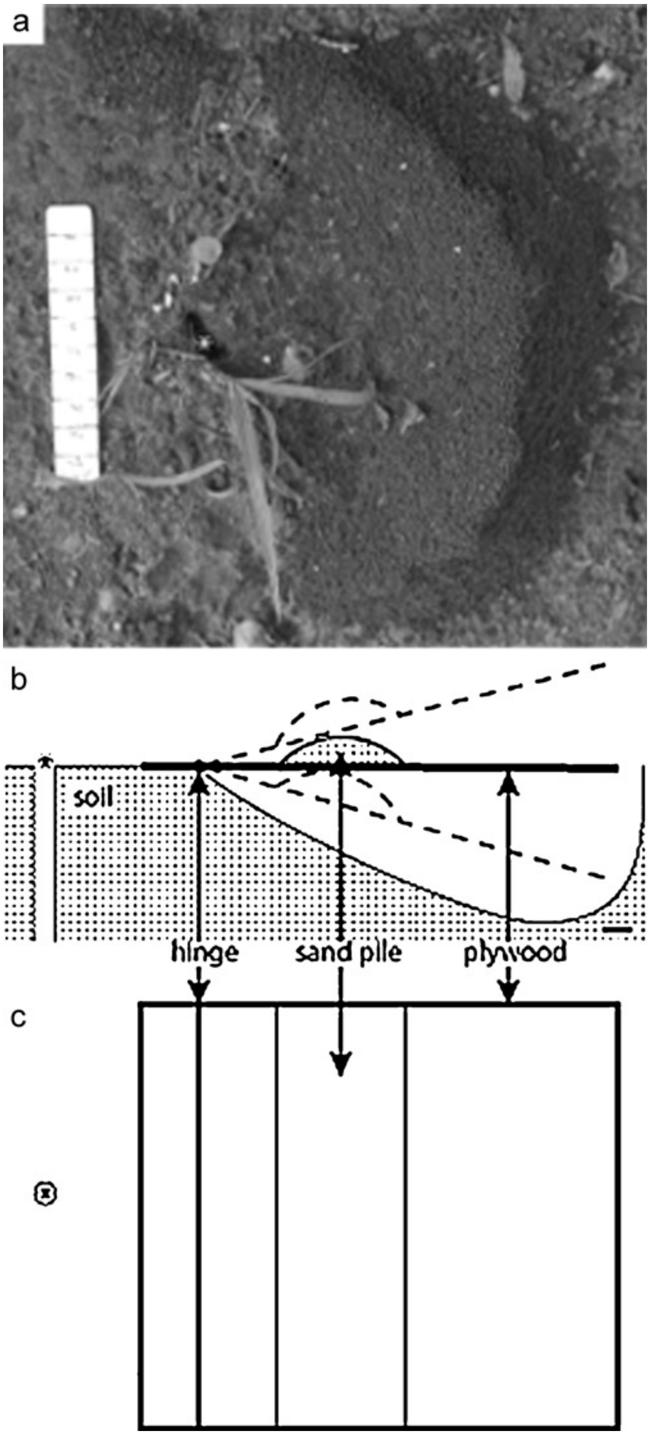

Figure 1. Natural sand pile (a) and experimental set-up for studying the effect of sand pile slope on load deposition by *Pheidole oxyops* ants viewed from the side (b) and top (c). The experimental sand pile is on a piece of plywood connected by a hinge with another piece of plywood which is fixed next to the colony's nest entrance. This allows the sand pile to be tilted up or down (dashed line). Position of the nest entrance is marked with asterisk. The scale bar 10 cm (a) and 1 cm (b); Figure c is the same scale as b.

Results

Platform tilted down

After tilting down, the ants deposited their loads closer to the nest entrance than before (ANOVA: $F_{1,2475} = 64.51$, $P < 0.001$). Relative position declined by 0.072 from 0.530 ± 0.006 (mean $\pm$ SE; $N = 1162$) to 0.458 ± 0.007 ($N = 1323$, Fig. 2). Relative positions differed significantly among colonies (ANOVA: $F_{4,2475} = 377.59$, $P < 0.001$, Fig. 3) but all colonies reacted similarly by dumping closer to the entrance (interaction between colony and tilting factors non-significant, ANOVA: $F_{4,2475} = 0.53$, $P = 0.712$, Fig. 3).

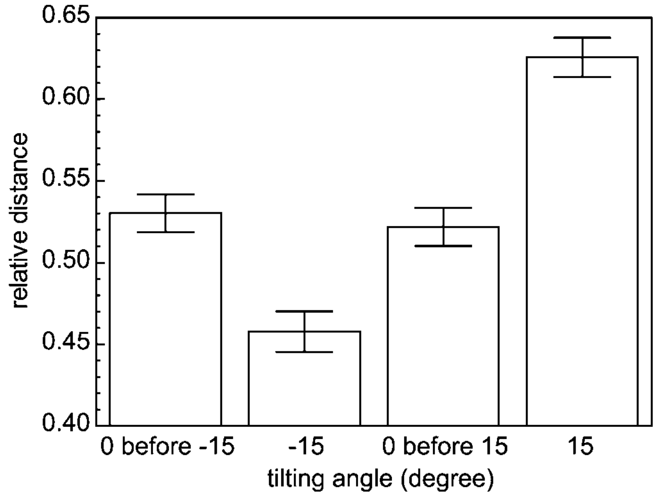

Figure 2. Relative distances of load deposition by individual ants when the sand pile was level (0 degrees), tilted down (–15 degrees) or tilted up (+15 degrees). Tilting the pile down resulted in load deposition at a smaller mean distance from the nest entrance and tilting up resulted in load deposition at a greater mean distance from the nest entrance.

During the 15 minutes that the platform was level before tilting down, dumping became more distant from the entrance with time (i.e., the relative position increased) in 2 of the 5 colonies. However, the correlation was significant in only one colony (Table 1). During the 15 minutes that the platform was tilted down, in all 5 colonies there was a trend for dumping to occur closer to the entrance. However, this trend was not significant in any of the 5 colonies (Table 1).

Platform tilted up

After tilting up, the ants deposited their loads further away from the nest entrance (ANOVA: $F_{1,2328} = 160.45$, $P < 0.001$). Relative position increased by 0.104 from 0.522 ± 0.006 ($N = 1249$) to 0.626 ± 0.006 ($N = 1089$) (Fig. 2). Relative positions differed significantly among colonies (ANOVA: $F_{4,2328} = 500.76$, $P < 0.001$, Fig. 3). There was a significant interaction between colony and

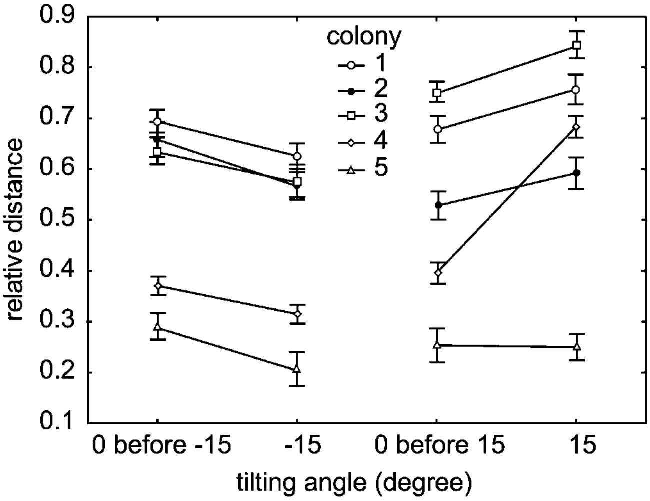

Figure 3. Relative distance of load deposition by ants from five colonies when the sand pile was level (0 degrees), tilted down (–15 degrees) or tilted up (+15 degrees). The distance at which ants deposited their loads differed between colonies, but tilting the pile down resulted in 5 out of 5 colonies depositing closer to the nest entrance and tilting up resulted in 4 out of 5 colonies depositing further from the entrance.

tilting factors (ANOVA: $F_{4,2328} = 45.25$, $P < 0.001$, Fig. 3). In one colony relative distance decreased slightly but non-significantly, but in the other 4 colonies relative distance increased (Fig. 3).

During the 15 minutes that the platform was level before tilting up, dumping became more distant from the entrance with time (i.e., the relative position increased) in 2 of the 5 colonies. However, neither of these correlations was significant. Only when the data from all 5 colonies were pooled did the positive correlation between time within the 15 minute period and dumping position become significant (Table 1). After tilting the platform up, dumping became more distant from the entrance in all 5 colonies but this relationship was significant only in 2 of the 5 colonies (Table 1).

Discussion

Our results show clearly that the slope of the sand pile affects dumping position in the predicted way in *Pheidole oxyops.* That is, when the pile is tilted down dumping occurs closer to the nest entrance, and vice versa. Although there were significant differences between colonies (Fig. 3), in only one of the 10 trials was the trend in the dumping position not as predicted. However, this trend was non-significant. These results strongly support the hypothesis (Tofilski and Ratnieks, 2005) that individual ants detect the slope of the pile and dump in relation to this.

The magnitudes of the changes in dumping position (0.10 up and 0.07 down) were close, although lower, to that expected (0.12) from the prediction that the position would remain constant in terms of the angle of slope. This indicates that other factors affect the dumping position. One possibility is that ants also remember the distance walked from the entrance and during consecutive trips tend to deposit their load at similar distance. Or have an inbuilt preferred distance. Such behaviour is predicted by template hypothesis. This suggests that *P. oxyops* use both self-organization and template mechanisms in sand pile building. The use of a template mechanism may also be important in the initiation of a sand pile at a particular distance, and possibly direction, from the nest entrance. However, when the sand pile has been formed the simple rules based on slope to a large degree determine the place of load deposition.

The position of load deposition, when averaged across colonies, was, as we expected, close to the apex of the pile. There was, however, large variation both within and between colonies. In some colonies a significant proportion of the loads were deposited on the inner slope. If this persisted it could have resulted in sand particles rolling towards the nest entrance and also in the sand pile extending towards the nest entrance. In natural piles of *P. oxyops*, load deposition occurred mainly near the top of the sand pile and if the sand particles rolled they always did so away from the nest entrance (pers. obs.). This discrepancy was probably caused by the relative flatness of the experimental sand pile when

Table 1. Correlations between time and relative position of load deposition in the five study colonies of *Pheidole oxyops.* Correlations are given for loads dumped during the 15-minute level period before the pile was tilted down (angle = 0 before –15) or up (angle = 0 before + 15 degrees), and the following 15-minute down (angle = –15) or up (angle = + 15) period

Colony	angle (degrees)							
	0 before –15		–15		0 before +15		+15	
	r	P	r	P	r	P	r	P
1	0.173	0.003	–0.029	0.654	–0.051	0.453	0.063	0.413
2	–0.054	0.431	–0.125	0.133	0.041	0.427	0.149	0.030
3	–0.008	0.864	–0.013	0.781	–0.015	0.781	0.020	0.713
4	–0.057	0.400	–0.100	0.254	–0.044	0.615	0.315	< 0.001
5	0.071	0.432	–0.121	0.084	0.043	0.557	0.013	0.872
all	0.049	0.076	–0.035	0.232	0.074	0.008	0.011	0.721

compared with the natural situation. In addition, on the experimental sand piles it was probably more difficult for ants to detect the sand pile apex, as there was no abrupt change in angle.

It is not clear why *P. oxyops* ants build their piles on one side of the nest entrance and relatively far away from it, rather than is a circular crater close to the entrance. This does not agree with the cost minimization hypothesis proposed by Franks et al. (2004) as the least costly sand pile is circular and close to the nest entrance. However, ant colonies may have to balance more than one cost and benefit. Because *P. oxyops* entrances are also used for foraging and because large insect prey are sometimes collected (pers. obs.), having a pile on just one side of the entrance is probably adaptive in not impeding foraging. Building the sand pile at a distance from the entrance may also reduce the possibility that heavy rain, which was common at the study site, will wash the excavated material back into the nest entrance.

It has been suggested that ants build sand piles around their nest entrances using an internal template (Theraulaz et al., 2003). The template can be within the insect brain and determine the shape of the sand pile. This explanation, although possible, may be disadvantageous in unpredictable environments. Self organization based on simple rules probably allows greater flexibility, by allowing the ants to adjust their behaviour according to the local environment. For example, ants might walk further to dump if there was a local area of upward slope. When ants follow the simple rule of load deposition based on slope, most soil will be dumped beyond the apex of the pile and the inner slope will never become too steep and unstable (Tofilski and Ratnieks, 2005). But if ants deposit the load according to a fixed template the sand pile becomes steeper with time and at some point might collapse towards the nest entrance. However, it is also possible that self organization and a template can combine. In *P. oxyops*, the pile is built some distance from the entrance. Perhaps the ants have an internal template that causes them to initiate dumping 10–15 cm from the entrance. If this were combined with the tendency to dump on outer slopes, this would be sufficient both to generate the shape of the observed piles and their position in relation to the entrance.

Applying the simple rule of depositing excavated soil where the slope changes from up or flat to down may well be a common mechanism used by ants in general, especially for species that build steep-sided piles, whether circular or not, of excavated material. Steep-sided piles with dumping near the apex are also known in *Myrmica ruginodis*, *Camponotus compressus* (Sudd, 1977), *Dorymyrmex* (Tofilski and Ratnieks, 2005), and *Pheidole ambigua* (Robinson, 2006), as well as many other ants at Fazenda Aretuzina including *Atta* and *Acromyrmex* (personal observations). Although our study makes a significant contribution to understanding the rules by which ant colonies form sand piles, our results also indicate that it is likely that pile formation depends upon more than one mechanism even in a single species of ant. Further studies are needed to investigate the full set of rules and mechanisms used by any one species in forming piles, and how these can be modified to form dumps of different geometry, or indeed how different rules and mechanisms can give piles of the same geometry.

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Appendix: calculation of position of the sand pile apex

The apex of a level experimental pile is mid way between the inner and outer edges. But when the pile is tilted the position of the apex changes. The new position can be calculated by rotating the cross section of the sand pile by the tilt angle α (Fig. 4). The distance, *a,* between the inner edge of the pile and the apex is

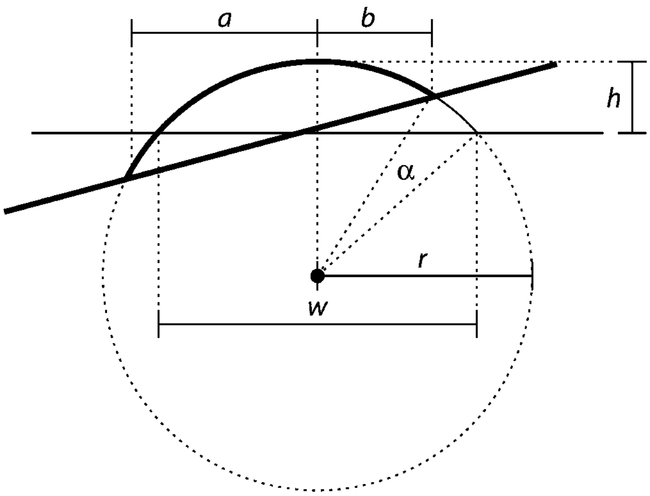

Figure 4. Vertical cross section of the sand pile before tilting (thin line) and after tilting 15 degrees (thick line). *a* – distance between the front of the tilted sand pile and its top, *b* – distance between top of the tilted sand pile and its back, *h* – height of the sand pile, *r* – radius of the imagery cylinder used to form the sand pile, *w* – width of the sand pile; *α* – tilting angle.

$$a = \frac{w}{2}\cos(\alpha) + (r - h)\ \sin(\alpha)$$

and the distance *b* between the apex of the pile and its outer edge is

$$b = \frac{w}{2}\cos(\alpha) - (r - h)\ \sin(\alpha)$$

where *w* is pile width, *h* pile height, α the tilt angle, and *r* the radius of the circle used to construct the cross section of the pile. The relative position of the apex of the pile *t* equals $t = a/(a + b)$. In the current experiment, the positions of the apex when the pile is tilted up by 15 degrees and tilted down by 15 degrees are 0.62, and 0.38, respectively.