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Physical properties of casts of the earthworm *Aporrectodea rosea*

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Summary. Some physical properties of casts of the earthworm *Aporrectodea rosea* were examined and compared with the properties of aggregates from the bulk soil. Cast shape was quantified by three ratio methods and two mathematical spectra methods, using data obtained by two-dimensional scanning. Shapes were compared with previously published descriptions of "modexi". The tensile strength of dry casts was measured by the indirect tension method and was found to be approximately 2.5 times greater than that of dried aggregates of similar size. Tensile strengths are used to predict that beds of casts are less compactable than beds of aggregates. From relationships between soil water content, matric potential and undrained shear strength of fresh earthworm casts, the mean pressure applied to soil as it is remoulded by passing through the earthworm gut is estimated to be 259 Pa.

Key words: Earthworm Casts – "Modexi" – Shape – Tensile strength – Pressure – *Aporrectodea rosea*

The shape of soil particles has received some quantitative attention since the advent of micro-computers (Davis and Dexter 1972; Dexter 1985), but micro-computer techniques have not been applied specifically to how soil particles are influenced by the soil fauna. Surface casts formed by earthworms have been described as either ovoidal or sub-spherical to spherical pellets, or as paste-like slurries (Lee 1985).

Bal (1973, 1982) used the term "modexi" (from "moulded" and "excrement") for excrements which have left the animals' intestines as three-dimensional shaped individuals. Modexi were classified by Bal according to their shape; size; mineral, organo-mineral or organic composition; basic distribution (whether embedded or not) and related distribution. He defined five basic shapes: spherical, ellipsoidal, cylindrical, platy and threadlike (mitoid). Each of these shapes was subdivided into one to three subgroups, e.g. ellipsoidal into ellipsoid, spermoid or conoid. He also noted that the shape of modexi can be transformed by ageing or by physical or chemical effects, so that shape descriptions can indicate whether a system has been transformed weakly, moderately or strongly.

The breakdown of earthworm casts is determined by their tensile strength, which determines their reactions to treading by animals, compaction by vehicles and raindrop impact, and their water stability. Wet-sieving techniques have been used (Swaby 1950) to gauge the stability of casts, but the tensile strength which determines mechanical breakdown has received no attention.

Wolf (1940) found from manometric tests that fluid was extruded into a cannula at the mouth of *Lumbricus terrestris* until a maximum pressure of approximately 450 Pa was reached. The pressures inside the coelom of *L. terrestris* have been measured by Trueman (1978) at less than 200 Pa when the worm is at rest. Newell (1950), using capillary manometers and spoon gauges, showed the average coelom pressure was 1.6 kPa in the anterior third of active *L. terrestris* and 0.8 kPa in the tail region. The pressure in narcotized worms was found to be zero. He noted that the manometric readings did not show the rapid fluctuations in pressure which occur during wriggling movements of worms.

These internal pressures of earthworms are much lower than the maximum pressures which worms can exert during burrowing. The ability of earthworms to push particles aside has been estimated from their ability to lift a "bridge" under which they were re-

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quired to move by Seymour (1978), who showed that pressures exerted by *L. terrestris* reached a maximum of about 7500 Pa. The ability of earthworms to burrow into compacted soil was examined briefly by Dexter (1978), who found that, for *Aporrectodea calignosa,* there was no significant correlation between the total length of tunnels made in blocks of Urrbrae loam and the strength of the block over the range of penetrometer pressures 0.3 – 3.0 MPa.

When an earthworm is burrowing, the anterior end of the body is forced into crevices and the gap may be widened by the inflation of the body. Newell (1950) did not record pressures during this phase of activity, but anticipated that they would probably be much higher than those obtained during wriggling, because they would be due to the contraction of the longitudinal muscles of the body wall, which are far more bulky than the circular muscles.

Much of the previous work on earthworms and soil structure has been concentrated in areas with large earthworm populations and rainfall well in excess of that occurring in the Mediterranean type of climate of southern Australia. The notable exceptions are the studies of Barley (1959 a, b), who considered the rates of casting and the chemical properties of casts, and Humphreys (1981), who compared rates of ant mounding with earthworm casting, including some measurements of cast size and qualitative shape analysis. Our work considers the application of recent mathematical shape description to biologically influenced systems and provides quantitative data on the physical properties of worm casts produced by a locally common species (*A. rosea*).

Materials and methods

The earthworms used in these experiments were collected from the A horizon of the Urrbrae sandy loam of the Red-brown Earth Group (Oades et al. 1981) at the Waite Agricultural Research Institute, Glen Osmond, South Australia. This soil has 17% clay (<2 μm), a plastic limit of 19.5% and a liquid limit of 26.5%. The site has a Mediterranean type of climate with a warm dry summer and a cool wet winter. Soil temperatures at 15 cm depth range from a mean daily maximum of 30.3 °C in January to a mean daily minimum of 9.7 °C in July (W. A. R. I., 1984). Because of the dry summer, earthworms are active for only about 6 months of the year (Barley 1959 b).

Earthworms of the species *Aporrectodea rosea* were collected in winter. *A. rosea* is a geophagous species which was introduced to Australia from northern Europe. Identification was based on the taxonomic keys of Lee (1959 a) and Martin (1977), using the index to specific names of Easton (1983). Collected worms were stored in bins containing the Urrbrae soil and kept in a growth cabinet at 15 °C night and 20 °C day until needed for the experiments. All experiments were done in a laboratory maintained at approximately 20 °C.

The shape of earthworm casts was determined by placing adult earthworms in sieved (<2 mm) soil on sintered glass funnels. The funnels were connected by a hanging column of water to a reservoir to maintain a constant matric potential of −5 kPa. After allowing several days to accliminatize the earthworms, they were gently removed from the soil and held by hand above a microscope slide until they excreted a cast or until they became agitated. The cast was immediately photographed by a camera attached to a binocular microscope at 10× magnification. The excreted material maintained its integrity during the photography. The approximate dimensions and the weight of each cast were determined.

From the photographs, outline tracings were made of the cast shape. These tracings were then scanned automatically with a television camera which was connected to a digitizer and micro-computer using the method of Dexter (1985). From the digitized outlines, three simple ratio methods and two mathematical spectrum analyses were performed. The spectrum methods were the Fourier analysis of a radius vector within a particle (Schwarcz and Shane 1969) and the curvature spectrum of Davis and Dexter (1972). As a comparison, about 20 air-dried aggregates were collected from gently sieved (>1 mm and <2 mm) soil and similarly photographed and scanned. The aggregate size range used was similar to that of the casts but none appeared to be recent biologically influenced material.

Adult earthworms were placed in soil at known matric water potentials for tensile strength determinations. For the range of potentials −1 kPa to −10 kPa, earthworms were placed in soil on a sintered glass funnel as described above. For the more negative potentials (−30 and −50 kPa), the soil was equilibrated using a pressure plate apparatus and then placed in sealed tins along with earthworms. Every 2 – 3 days the tin lid was removed briefly to allow air exchange. After 10 days the earthworms were removed from the funnels and tins and the soil left for a further 5 days. This period was selected to permit all casts adequate time for age hardening. Utomo and Dexter (1981) found that after 5 days of ageing there was little change in the penetrometer resistance of Urrbrae loam. The soil was then removed onto trays and the casts carefully sorted using a fine brush. The casts obtained were allowed to air-dry for 24 h, then were oven-dried at 105 °C for 24 h. Tensile strengths of the casts were measured using the indirect tension or crushing test (Rogowski and Kirkham 1976) for small or weak aggregates, as described by Dexter and Kroesbergen (1985). Briefly, this entails placing the sample between two flat parallel plates and applying a load which is measured on a pan balance. The size of the casts was measured using calipers. Aggregates were collected from the bulk soil in the field and sorted in the same manner as previously described. The tensile strengths of these aggregates were also determined after air-drying and oven-drying.

Croney and Coleman (1954) found an unique relationship between the water content of a continuously disturbed soil and its matric potential. In saturated soil this potential is equivalent to an equal external load on the soil. Using a small tensiometer equilibrated with a mercury manometer, this relationship was determined for the Urrbrae soil. Wet soil was placed in a small mixer and moulded. As soon as mixing ceased the tensiometer was inserted and a sample of the soil was taken for gravimetric water determination. A steady measurement of matric potential was obtained within about 3 min of cessation of mixing.

The undrained shear strength of the remoulded bulk soil was determined using a Geonor cone penetration apparatus as in the methods of Hansbo (1957) and Towner (1973). This relates the undrained shear strength, τ_f (Pa), to the depth of penetration, h (mm), of a cone into the soil by the equation

$$\tau_f = \frac{KQ}{h^2} \tag{1}$$

where Q (g) is the weight of the cone (which in these cases was 100, 80, 60 or 10 g) and K is the coefficient dependent on the cone angle β. For the heavier cones, i.e. 100 and 80 g, where the cone angle is

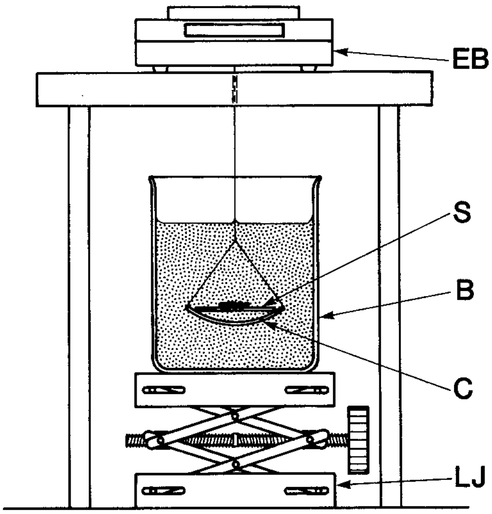

Fig. 1. Volume determination for fresh earthworm casts. A pre-weighed slide (*S*) onto which an earthworm cast has been excreted rests on the cradle (*C*), which is attached by a free line to the electronic balance (*EB*). Kerosene in the beaker (*B*) is raised around the cradle by means of the laboratory jack (*LJ*)

30°, K for a sandy loam takes the value of 1.6×10^4 (Towner 1973). For the lighter cones with cone angles of 60°, τ_f was taken directly from tables for disturbed soil given in Hansbo (1957) and in the Cone Manufacturer's Handbook (Geonor, Oslo, Norway). The soil gravimetric water content was determined for each cone penetrometer reading, enabling the shear strength to be directly related to the water content.

The total carbon contents of the casts and the bulk soil were determined by dry combustion in a furnace using a Leco CR-12 carbon system. The surface layer of the Urrbrae sandy loam lacks carbonate (by acid treatment), and therefore the organic matter content can be estimated by multiplying the carbon content by a factor of 1.72.

The dry bulk density and voids ratio of the 'wet' casts were determined as follows: Earthworms were kept in soil on sintered glass funnels as previously described. Casts from the hand-held earthworms were excreted onto a pre-weighed slide which was then transferred to a cradle hanging below a balance (Fig. 1). Kerosene in a beaker was raised by a moveable platform to a set height around the cradle and the change in balance reading noted. The density of kerosene and the displacement of the cradle and slide had been determined previously. Thus the volume of the wet cast was found by subtraction. The cast was then oven-dried and the dry weight taken to establish the gravimetric water content. The wet casts appeared saturated and no air was seen to leave the casts when in the kerosene.

Results and discussion

Shape

The centroid, area and perimeter were calculated by computer from the digitized outlines. From these, the ratios shown in Table 1 were determined. Roundness is

$$\frac{4\pi \text{ (area)}}{\text{(perimeter)}^2} . \qquad (2)$$

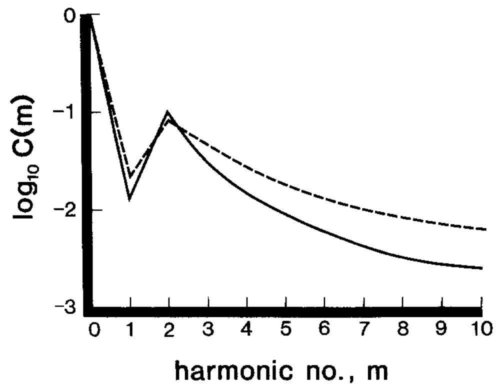

Fig. 2. Plots of the normalized radius spectra ($C(m)$) against the harmonic number (m). Curves are the envelopes of the mean, smoothed, discrete values for casts from *A. rosea* (*solid line*) and the similar size aggregates of Urrbrae loam (*broken line*)

Table 1. Roundness and aspect ratios of casts and similar-sized field aggregates

	Casts	Aggregates
Roundness*	0.795 (0.019)	0.650 (0.014)
AR 90°	0.674 (0.053)	0.717 (0.028)
AR_s	0.705 (0.038)	0.649 (0.026)

Figures in parentheses are SEs
* Roundness figures are significantly different at the $P < 0.01$ level

If D_{max} is the maximum diameter of the cast or aggregate, then the right angle aspect ratio is the ratio of D_r to D_{max}, where D_r is the diameter through the centroid at right angles to D_{max}

$$AR_r = \frac{D_r}{D_{max}} . \qquad (3)$$

The shortest aspect ratio, AR_S, is the ratio of the shortest diameter, D_S, which passes through the centroid, to D_{max}

$$AR_S = \frac{D_S}{D_{max}} . \qquad (4)$$

The radius spectra (Fig. 2) and the curvature spectra (Fig. 3) both show that the casts are rounder than soil aggregates of similar size. The casts used in our work comprise a number of shape classes as described by Bal (1973), including both spheres and amoebospheres, ellipsoids and bacillo and clonocylinders. Neither platy nor mitoid forms were observed. Within the size classification scheme of Barratt (1969) as modified by Bal (1973), the wet casts were all greater than 2.5 mm along their longest axis, placing them as either macro-excrements or coarse micro-excrements.

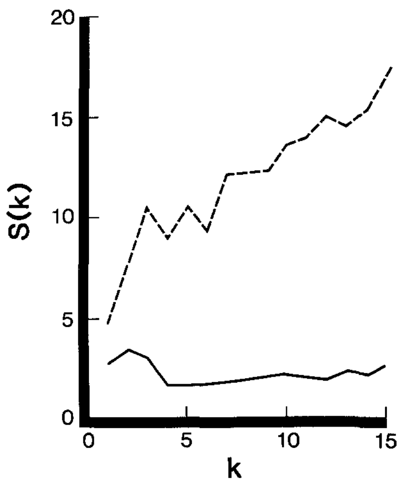

Fig. 3. Plots of the curvature spectra ($S(k)$) for different values of k. *Curves* are the envelopes of the 3-point running mean, discrete values for casts from *A. rosea* (*solid line*) and the similar-sized aggregates of Urrbrae loam (*broken line*)

When classifying modexi (or casts), Bal (1973) noted that the shape may be transformed as a result of ageing and used the terms weakly, moderately and strongly to describe the degree to which breakdown has taken place. The spectra measurements described above could be used to obtain quantitative values for the amount of transformation if the initial modexi were known. Thus the techniques described here could be used to study the breakdown of casts in the field and consequently the importance of physical processes leading to their eventual demise could be estimated. Furthermore, the shapes and relative numbers of modexi could lead to an assessment of the activity and numbers of earthworms, or other soil fauna species, involved in soil modification.

Carbon

Total carbon content of the casts was 1.64%, compared with 1.54% for the bulk soil. Only casts that had been photographed were combined to provide enough material for the carbon test, so that no replication was possible. These values correspond to approximately 2.8% and 2.6% organic matter, respectively, as the soil is carbonate free, and are markedly different from the 8.3% and 4.8% organic matter reported by Czerwinski et al. (1974) from casts and bulk soil in a Polish grazed pasture with the same earthworm species. The differences in the organic matter in the casts may be attributed to the higher organic content of the bulk soil which would permit more selective "grazing" by the worms.

Tensile strength

From the crushing force (F (N)) as measured on the balance and the diameter (d (m)) of the cast, the tensile strength is calculated from

$$Y_C = \frac{0.576\,F}{d^2}, \tag{5}$$

which assumes that the particle is spherical (Dexter and Kroesbergen 1985). Figure 4 shows the relationship between matric potential at which the cast was produced and the tensile strength. Potentials more negative than −50 kPa were tried but the earthworms went into a state of anhydrobiotic quiescence. While this is a less negative potential than reported for some species (Lee 1985), laboratory conditions would not be ideal for earthworm activity. It is apparent that the tensile strength of casts is greater than the tensile strength of similar-sized aggregates, irrespective of the potential at which the casts were generated. Although not reasons for additional strength are apparent from our work, Swaby (1950) attributed increased stability of casts to microbial gums produced by bacteria or by fungal hyphae from the worm gut. Over the range −1 to −30 kPa matric potential, the strengths do not differ significantly. At −50 kPa matric potential, a significant increase in tensile strength is observed. The mean mass of the dry casts used for the strength determination was 0.0055 g (SE 0.0002) and the mean length along the longest axis of the cast was 2.20 mm (SE 0.025). There was no change in the estimated dry cast density with the matric potential at which they were formed, so the increased strength at the most negative potential was not due to density differences. The increased tensile strength may be caused by a modification in water extraction from the soil in the gut at larger negative potentials, but physiological experimentation would be required to test this.

Lee (1959b) drew attention to management problems when large numbers of surface-casting earthworms were very active in pastures in New Zealand. Treading by grazing animals caused the accumulated surface layer of casts to compact, burying the crowns of pasture grasses and resulting in the death of plants. The model for the compaction of beds of soil aggregates proposed by Braunack and Dexter (1978) can be used to estimate the reduction in height of a bed of aggregates during compression. This model is

$$\frac{H}{H_i} = 0.4 + 0.6\exp\left[0.017\left(\frac{P}{Y}\right) - 0.38\left(\frac{P}{Y}\right)^{1/2}\right], \tag{6}$$

where H is the final sample height, H_i is the initial height of the bed of casts, Y is the tensile strength of

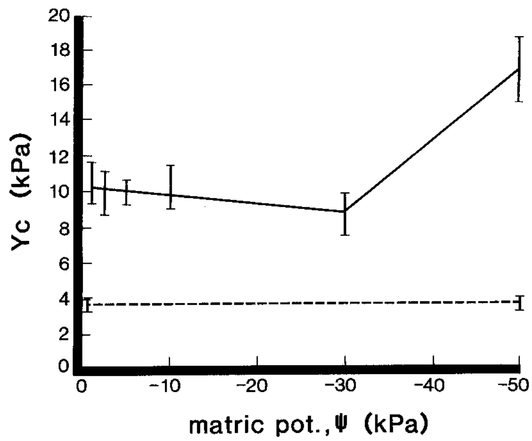

Fig. 4. Tensile strength (Y_c (kPa)) of dry casts from *A. rosea* (*solid line*) as a function of the matric potential [Ψ (kPa)] of the bulk soil from which the casts were produced. The tensile strength of aggregates collected from the field and then dried (*broken line*) are shown for comparison. *Error bars* are 2x standard error

the aggregates comprising the bed, P is the applied load.

If the pressure applied by the hooves of sheep is estimated at 80 kPa (Willatt and Pullar 1983) and the tensile strength of dry casts is taken to be 10 kPa (Fig. 4), then Eq. (6) shows that the final height of the bed will be 0.63 of the initial height. The same method of calculation can be applied to beds of aggregates with a tensile strength of approximately 4 kPa (Fig. 4). In this case, the final height of the bed will be 0.55 of the initial height. Thus the increased tensile strength of casts compared to aggregates may limit compaction in agricultural situations at least with the dry soil aggregates and casts considered here.

Forces in cast production

The relationship between the gravimetric water content (w%) and the matric potential (Ψ(Pa)) of the freshly-moulded soil, as determined with a rapid response tensiometer, is

$$\log_e|\Psi| = \underset{(0.37)}{13.58} - \underset{(0.017)}{0.300}\ w\% \quad (7)$$

with 96% of the variance accounted for. Similar responses were first reported by Croney and Coleman (1954). Values in parentheses are standard errors. Similarly, the relationship between the undrained soil shear strength, τ (Pa), and the gravimetric water content determined by the drop cone method of Hansbo (1957) is

$$\log_e|\tau| = \underset{(1.10)}{19.24} - \underset{(0.042)}{0.520}\ w\% \quad (8)$$

with 80.6% of the variance accounted for. Casts collected from earthworms (*A. rosea*) in soil at a matric potential of −5.0 kPa had a mean bulk density of 1.15 (SE = 0.06) g ml^{-1} and a mean gravimetric water content of 32.0 (SE = 2.9)%. By substituting each individual water content for each cast into Eq. (7), a mean value of 259 (SE = 93) Pa is obtained. Thus the mean maximum pressure applied to soil as it passes through the gut of the earthworm *A. rosea* is 259 Pa. The highest individual pressure achieved was 742 Pa for a cast with 23.2% gravimetric water content. It must be noted that as Eq. (7) is logarithmic, the substitution of the mean water content gives the geometric mean rather than the arithmetic mean of the pressures. The pressure values achieved in the coelom of other earthworms (*L. terrestris*) were estimated at <200 Pa by Trueman (1978) for resting worms, and at 1.6 kPa in segment 28 of active *L. terrestris* and 0.8 kPa near the tail region of *L. terrestris* by Newell (1950). Thus, even for different species, it appears that the pressure in the coelom is of similar magnitude to the maximum pressure on the ingested soil as it is moulded.

Newly formed casts of *A. rosea* are predicted from Eq. (8) to have extremely low shear strengths. Again due to the non-linearity of the equation, the predicted value of 364 (SE 163) Pa is the mean for individual casts after substitution into the equation rather than the value obtained by substitution of the mean water content. The maximum shear strength for a fresh individual cast is estimated at 1310 Pa. These pressures exerted by the earthworms on the ingested soil are far lower than the maximum pressures they can exert when pushing soil particles out or their path. This difference is almost certainly a result of the different musculature acting in each case. The earthworm has a layer of circular muscle fibres and, internal to these, a layer of longitudinal muscles. These are responsible for extension and contraction of the segments respectively. The gut also has two muscle layers, an outer layer of longitudinal fibres and an inner layer of circular fibres, which are responsible for the movement of food but which are much weaker than the locomotive muscles. Consequently it is not surprising that the pressures exerted on ingested soil, as found here, are less than the maximum external pressures exerted by earthworms.

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