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Scaling in Tensile "Skeletons": Structures with Scale-Independent Length Dimensions

Abstract. *Skeletal structures that resist only tensile forces can scale differently than compression resisting structures that fail in bending or buckling. The tensile structures examined scalelike simple ropes: length and diameter of the structure are not correlated, and in three of four cases, length is independent of scale or load, but diameter is dependent on scale. These relations suggest that similarity in stress rather than strain, or deformational behavior, is the basis for mechanical adaptation in the gross dimensions of these tensile structures.*

Skeletons resist forces in the environment as well as forces generated by the organism. Some skeletal tissues, such as wood and bone, are rigid and resist both tension and compression; others, such as tendons and some plant stalks, are fibrous, flexible, and resist only tensile loads. The support system of most higher organisms combines tensile, compression resistant, and pliant elements (*1*). The combination of these elements in a particular skeleton reflects the size, behavior, and evolutionary history of the organism. One aspect of the size component in skeletal design that can be somewhat isolated from the other components is scaling—the adaptation of skeletal dimensions to the magnitude of environmental forces or the mass of the organism (*2, 3*). Modes of mechanical failure underlie most models and empirical studies of scaling, and scaling criteria have been based on similarity in stress (that is, force per unit of cross-sectional area of the skeletal element is constant throughout the size range, so that the diameter of the element is proportional to the load) or in strain (that is, deformation in length and diameter remains proportional to load; this might be termed a "work-to-break" criterion) (*2, 4*). Models for rigid skeletons based on either stress or strain criteria require similar scaling relationships, only the predicted exponents differ. Rigid, compression resisting skeletons scale so that (i) the length (y) and the diameter (x) of the elements are correlated and related by the allometric equation $y = ax^b$, where a is a constant and b has a value between 0.5 and 1.0, and (ii) both length and diameter scale with load or body mass (*2, 4, 5*).

The scaling of tensile skeletons can be significantly different from that of bones or other rigid elements. Galileo noted that the length of a tensile structure, such as a rope or cable, may be independent of diameter and load (*6*). Stress in a tensile element is a function only of its diameter and the load. If stress is the criterion of similarity, (i) biological tensile "skeletons" should exhibit variation in length which is independent of diameter, and (ii) diameter should scale with load, but length should be independent of load. In contrast, if strain energy or the deformation under load is the criterion of similarity, then (i) variation in length and diameter should be correlated, and (ii) both dimensions of the element should scale with the load.

We examined the scaling of length and diameter in four tension resisting structures (Fig. 1). In all but one case the relationships of the skeletal dimensions and estimates of the tensile loading were also examined. Whether there are scaling relationships among length, diameter, and load can be evaluated from the correlation coefficient. The scaling relationships are described by the least squares fit of the data, in logarithmic form, to the allometric equation. The

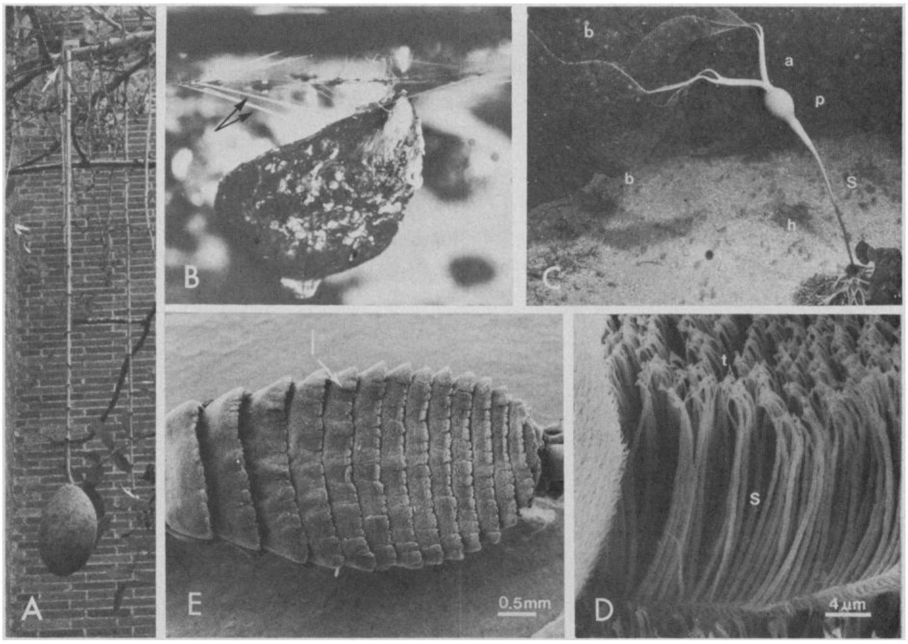

Fig. 1. (A) The stalk and fruit of the sausage tree, *Kigelia pinnata*; the arrow indicates the attachment of the stalk to the tree branch. (B) The blue mussel, *Mytilus edulis*, suspended from a glass plate by byssus threads (black arrows) that are independently cemented to the substrate and arranged like guy wires. (C) The elk kelp, *Pelagophycus porra*. The rootlike holdfast (*h*) anchors the plant to the sea floor; the blades (*b*), which can be as long as 12 m, stream out from the "antlers" (*a*); the antlers join at the gas-filled pneumatocyst (*p*); and between the "float" and the holdfast is the long, extensible stipe (*s*). (D) The subdigital hairs or setae of *A. evermanni*. Body weight is suspended from the spatulate setae tips (*t*) by the long stalks (*s*); the mechanism involved in grip is not known (*13*). This is a ventrolateral view of the setae taken near the distal edge of a lamella with the claw toward the right; note the variation in stalk length. (E) The adhesive toe pad of *Anolis cristatellus*, consisting of modified scales or lamellae (*l*); the claw (not shown) is toward the right.

scaling exponent b is reported with 95 percent confidence limits assigned from Student's t-table and the standard error of the slope.

1) The sausage tree, *Kigelia pinnata*, has a large, heavy, potato-like fruit that is suspended from the tree branch by a long panicle or stalk (Fig. 1A). The stalks are not stiff enough to support their own weight and are much more flexible and extensible than the tree branches. Total length and diameter of the stalk are not related (Fig. 2A). Stalk length is independent of fruit mass ($r = -.097$), but stalk diameter scales as (fruit mass)$^{0.361 \pm 0.069}$ (Fig. 3A).

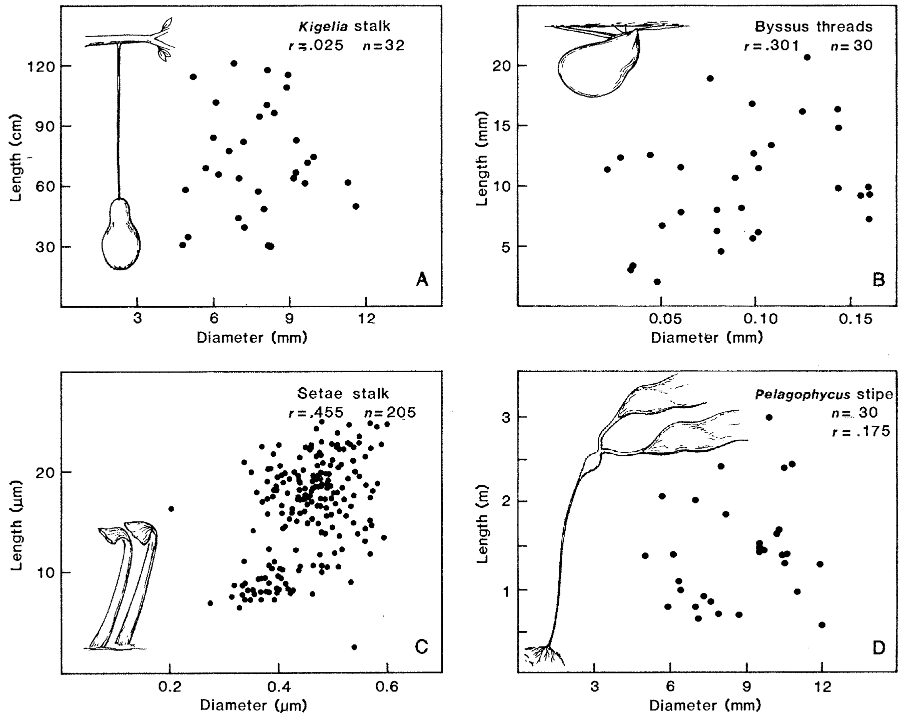

Fig. 2. (A) The relationship of *Kigelia* stalk length and minimum stalk diameter (measured to the nearest 1 mm and 0.1 mm, respectively). Minimum stalk diameter occurs near the midpoint of the stalk. (B) The relationship of *Mytilus* byssus thread length (measured to the nearest 0.1 mm) and diameter. The threads are ellipitical in cross section; the diameter is an average of the maximum and minimum diameters, measured to the nearest 0.01 mm on sectioned threads. (C) The relationship of *Anolis* setae stalk diameter and stalk height (measured to the nearest 0.002 μm and 0.1 μm, respectively). Measurements were made from scanning electron micrographs of a longitudinal section of the fourth (largest) toe pad and were taken along a proximo-distal transect of a mid-pad lamella, where most of the variation in dimensions occurs. The 205 setae represent approximately equal samples from the six species. (D) The relationship of total stipe length (measured to the nearest 1 cm) and minimum stipe diameter (measured to the nearest 0.1 mm just above the holdfast) in *Pelagophycus*.

2) The bay or blue mussel, *Mytilus edulis*, attaches to hard surfaces in the intertidal and subtidal zones by means of tough, extensible byssus threads (Fig. 1B) (*7*). The weight of the mussel and the forces exerted on the shell by currents and waves place tension on the threads. Length and diameter of the threads were not correlated in a sample of 30 mussels with shell lengths between 11 and 70 mm (Fig. 2B).

3) *Anolis* lizards, including the American chamaeleon, are able to adhere to vertical and overhanging smooth surfaces without using their claws. The body mass is suspended by a series of tensile structures that begins with the keratinous subdigital hairs or setae (Fig. 1D). The setae are borne on specialized subdigital scales called lamellae; and the series of lamellar scales forms a pad on each digit (Fig. 1E). We examined scaling in the dimensions of the seta stalk and pad in representatives of six *Anolis* species showing most of the body size variation within the genus (32 to 186 mm in our sample).

Seta stalk length and diameter are correlated (Fig. 2C), but the correlation coefficient accounts for such a small fraction of the variance that a mechanical similarity is probably not present. Mean stalk diameter and length for the individual specimens are not correlated ($r = .328$, $n = 12$). Stalk length varies between species but does not scale with body size ($r = .496$, $n = 12$). Stalk diameter is not significantly different among the six species [$F(5, 10) = 4.22$, $P >$

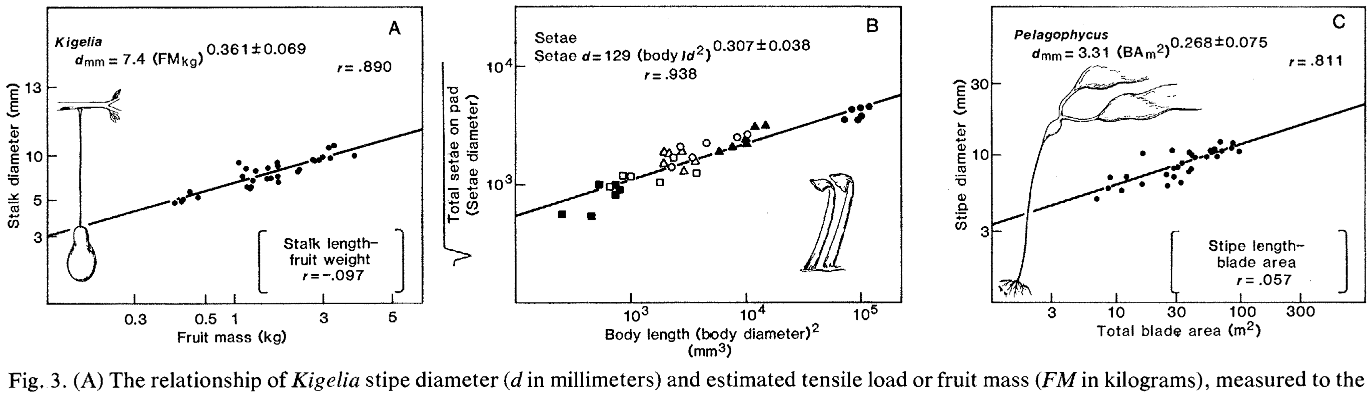

Fig. 3. (A) The relationship of *Kigelia* stipe diameter (d in millimeters) and estimated tensile load or fruit mass (FM in kilograms), measured to the nearest 10 g. The mass of the stalk constituted less than 2 percent of the fruit mass and was ignored in estimating the tensile load. The mean prediction error of this scaling equation relative to the observed points is 14 ± 3 percent (± 95 percent confidence limits). (B) The relationship of "diameter" (d) of the aggregate setae stalks and body size, estimated as snout-vent length × (trunk diameter)^2 or (body ld^2) in six species of *Anolis*. The diameter represented by all the stalks is computed from pad area (measured to the nearest 0.01 mm^2 from photographic montages taken normal to the pad) and seta density (measured as setae/150 μm^2). Seta spacing or density is not significantly different in different regions of the pad. The anole species are *A. cuvieri* (●), *A. evermanni* (▲), *A. cristatellus* (○), *A. stratulus* (△), *A. pulchellus* (□), and *A. occultus* (■). The mean prediction error for this allometric equation is 15 ± 4 percent. (C) The relationship of *Pelagophycus* stipe diameter (d in millimeters) and "drag," estimated from blade area (BA in square meters) when the coefficient of drag is a constant (*9*). Blade area is estimated from the total length and maximum width (measured to the nearest 2 cm) of the blades. The mean prediction error of this equation is 11 ± 4 percent.

.05]. Scaling in the functional complex appears to occur by variation in the number of stalks available to support the animal rather than by variation in the dimensions of the individual stalks. The diameter of the aggregate stalks can be estimated as (pad area × seta density)$^{1/2}$ since the individual stalk diameter is constant. The aggregate stalk diameter scales as (body size)$^{0.307 \pm 0.038}$ (Fig. 3B).

4) The elk kelp, *Pelagophycus porra*, has a long, flexible stipe that aligns with the direction of water flow (Fig. 1C). The stipe is subjected to tension by the buoyant float and more importantly by the drag on the large blades (*1*). The area of the kelp blades can exceed 100 m^2, and about 70 percent of the total drag on a similar kelp was due to drag on the blades (*8*). We measured the stipe length and diameter and the blade area of 30 intact, mature *Pelagophycus* growing at depths of 15 to 17 m. The length and diameter of the stipe are not correlated (Fig. 2D). We estimated tensile force on the stipe as drag on the blades. Assuming that water density (ρ) and the coefficient of drag (C_D) are constants, and that water velocity (V) is independent of scale and comparable for all plants, drag [$= 0.5(\rho V^2)C_D A$] is proportional to the total blade area (A). Stipe length is not correlated with blade area ($r = .057$), but stipe diameter scales as (drag or blade area)$^{0.268 \pm 0.074}$ (Fig. 3C). If we alter our assumption about the C_D, the changes in the exponent are relatively small (*9*).

These four examples represent a wide range of organisms from diverse evolutionary and ecological contexts, yet their scaling is similar. The length of the tensile structure in all cases is independent of diameter, and, in the three cases where we could examine scaling with tensile load, the length of the structure is independent of load or scale, but the diameter scales with load. Two general conclusions may be drawn. (i) The scaling relationships of these tensile structures are not consistent with the predictions of geometric similarity (length proportional to diameter, and both proportional to area$^{1/2}$ and mass$^{1/3}$), nor with the predictions of biomechanical models proposed for skeletal elements that resist bending and compression [for example, in elastic (strain) similarity, length proportional to diameter$^{2/3}$ and to mass$^{1/4}$; diameter proportional to mass$^{3/8}$ and to area$^{5/8}$] (*2, 4*). To our knowledge none of the skeletal structures investigated thus far exhibits scale-independent length dimensions (*2–5*). The scaling of tensile skeletons clearly can be different from that of rigid, compression resisting structures. (ii) The dimensions of the tensile elements (exclusive of the byssus threads) appear to reflect adaptation to maintain constant tensile stress rather than proportionality in strain or the work required to break the element (*10*).

There are a number of possible models based on stress similarity. If static tensile stress is constant, diameter should be proportional to (tensile force)$^{1/2}$ (since tensile stress = force/cross-sectional area). The observed exponents are closer to 1/3 than to 1/2, suggesting that static tensile stress is not the criterion for scaling in diameter. Much larger tensile forces could arise under dynamic conditions as the tensile force is applied through bending or torsional moments—for example, when wind produces swinging and rotation of the tree branch and sausage fruit, or when the kelp stipe is bent and twisted as currents change the orientation of the blades, or when the lizard toe is contacting and leaving the substrate. Tensile stress from a bending or torsional moment is proportional to the moment/diameter^3, suggesting that stress similarity is maintained if diameter scales as (bending moment)$^{1/3}$ or (torsional moment)$^{1/3}$. Assuming that bending force is proportional to static tensile load (for example, that the force bending the kelp stipe in the direction of water flow is proportional for any given deflection to the drag forces on the blades), the bending moment will be proportional to (force × stalk or stipe length). For the *Pelagophycus* sample, stipe diameter scales as (bending moment)$^{0.197 \pm 0.070}$ ($r = .732$), and for the *Kigelia* stalk, diameter scales as (bending moment)$^{0.247 \pm 0.072}$ ($r = .785$). Neither result is in good agreement with the predicted exponent of 1/3, and the correlation coefficients are lower than those for tensile load and diameter. Similarity in bending stress seems unlikely because of the low stiffness of the structures in bending and the poor correlation between length and diameter. Torsional moments could easily occur (for example, the *Kigelia* fruit is asymmetrical and rotates relative to the tree branch as it swings in the wind) and may be particularly threatening to fibrous materials such as the *Kigelia* stalk and kelp stipe, but additional data are required to examine the scaling of diameter with a torsional moment.

The structures we examined represent a diverse sample of tensile elements. In all cases the length of the structure is independent of its diameter, and in the three cases where we examined scaling with load, only diameter is correlated with load. The length of a tensile structure that scales in this way can be adapted to any ecological or behavioral variable independently of the load that must be resisted (*11*), but structures that resist compression and bending forces are constrained to scale length with load. Scale-independent length dimensions represent an additional degree of freedom in the design of a skeleton, which along with generally lower mass/strength ratios and minimal diameter (*1*) make tensile skeletons advantageous in a variety of contexts. Not all tensile elements, however, exhibit scale-independent length dimensions or stress similarity. Both the length and diameter of the Achilles tendon of mammals scale with body and muscle mass, suggesting a strain or deformational similarity (*12*). Even among tensile elements there are different scaling patterns. How a skeleton scales may reflect the properties of the biomaterial, the particular function of the structure, or both, but scaling relationships are clearly variable in the design of organisms.

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Form Movement (Reinhold, New York, 1963), p. 153].

10. Mechanical adaptation might be more complex if the properties of the biomaterial, such as *Young's modulus* (E), also scale with load. We cannot exclude this possibility, but even if the material properties are scale-dependent, strain or work-to-break similarity is unlikely given the consistently low correlation of length dimensions with load. Since strain energy or the work required to break an element is proportional to $E(ld^2)$, where l is length and d is diameter, ld^2 of the element should be correlated with the tensile load regardless of the scaling in E. This is not true for the elements we considered (for example, $r = .022$ for *Kigelia* stalk ld^2 and fruit mass).
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Detoxification Enzyme Differences Between a Herbivorous and Predatory Mite

Abstract. *The detoxification capabilities of the predatory mite* Amblyseius fallacis *and its herbivorous prey* Tetranychus urticae *are fundamentally different. The activities of mixed-function oxidase and* trans-*epoxide hydrolase are higher in the prey than in the predator; those of* cis-*epoxide hydrolase and glutathione transferase are lower; and esterase activity is similar. Dissimilarities may be related both to differing adaptations to plant allelochemicals and to the higher respiration rate of the predator. Hydrolytic and conjugating reactions appear more important than oxidative pathways in imparting organophosphate resistance to these acarines. These resistances provide insecticide selectivity favorable to the predator and improved integrated pest control.*

Soon after synthetic insecticides became widely used, arthropod pests developed resistance to them. Indeed, some pests were tolerant to these toxicants from the beginning. Herbivorous arthropod pests are consistently less susceptible to conventional insecticides than predators and parasites are (*1*). Insecticide resistance has been described in more than 400 species of pests compared with only 13 of their natural enemies (*2*). Greater insecticide susceptibility of the natural enemies and their reduced capability for resistance limits the effectiveness of pest control, especially that of integrated pest management, which combines pesticidal and biological controls.

Herbivores may be adapted to detoxify pesticides because they must detoxify plant secondary compounds (allelochemicals) in their diets. Much evidence indicates that allelochemicals are produced by plants to deter herbivores (*3*). In response, herbivores can increase detoxification enzyme activities that allow them to feed without suffering from allelochemicals. Mixed-function oxidases (MFO's), a major detoxification system in response to allelochemicals (*4*), also play a role in insecticide detoxification and resistance (*5*). Predators and parasites, which do not feed directly on plants, probably are less exposed to allelochemicals and thus may have lower MFO activities and be less adapted to detoxify or develop resistance to pesticides (*6*). Although predators and parasites may lack well-developed MFO's, they should be as adapted as their prey to the use of nonoxidative detoxification mechanisms, especially hydrolytic pathways (for example, esterases) (*7*) that also function in the basal metabolism of proteins and lipids.

We examined the detoxification enzymes of a pest and its natural enemy and found major differences (Table 1) that support the allelochemical adaptation hypothesis, yet demonstrate that for certain enzymes a carnivore can have an advantage over a herbivore in potential detoxification capability. A strain of the plant-feeding spider mite *Tetranychus urticae* (Koch) that is resistant to organophosphates and a strain that is susceptible to organophosphates were compared with a multiresistant (to organophosphates, pyrethroids, and DDT) and a susceptible strain of the phytoseiid predatory mite *Amblyseius fallacis* (Garman) (*8*). Study of both susceptible and resistant strains of each species allowed us to compare intrinsic detoxification potentials with enzyme modulation due to pesticide exposure.

The *T. urticae–A. fallacis* complex is a useful herbivore-predator model for comparative toxicology. The prey is polyphagous, feeding on more than 200 hosts. The predator is also polyphagous, but its native and principal host is *T. urticae*. Both mites cohabit in natural and agro-ecosystems. They have similar biologies, morphologies, and other characteristics (*6*). Susceptibilities to pesticides and plant toxins and the potential to develop resistance have been studied extensively in both mites (*9*).

Food-deprived mites were collected on a controlled-pore nylon filter that yielded an equivalent distribution of life stages (*8*). Large numbers of animals (10^3 to 10^5 individuals) were used to minimize age-related and other physiological variations that could decrease the reproducibility of results. Whole body homogenates were centrifuged at $12{,}000g$ to give a supernatant fraction suitable for a detoxification enzyme survey (*10*). Both phase 1 (oxidative and hydrolytic) and phase 2 (conjugative and epoxide-hydrating) reactions, that typify the metabolism of lipophilic toxicants (for example, pesticides and allelochemicals) to more polar and thus excretable products, were measured (*11*).

Aldrin epoxidase, a MFO, was measured by electron-capture detection of the product epoxide dieldrin (*12*). Epoxidation of pesticidal olefins, such as aldrin, by the action of the monooxygenase mediated by cytochrome P-450 is an index of the oxidative capability of the organism for lipophilic toxicants (*13*). In susceptible strains, the herbivorous prey mite had a fivefold higher MFO activity than the carnivore. This finding supports the hypothesis that a herbivore has a higher detoxification potential than its predator as a result of this important phase 1 enzyme group (*6*).

General hydrolytic capability was compared by the α-naphthyl acetate esterase assay, which measures activities of carboxylesterases, lipases, amidases, proteinases, cholinesterases, and thioesterases (*14*). No significant difference between the susceptible predator and susceptible prey mites was found, supporting the hypothesis (*7*) that arthropod herbivores and carnivores should have similar hydrolytic detoxification pathways because of the multiplicity of hydrolytic enzymes involved in endogenous metabolism.

Lastly, three phase 2 enzymes were surveyed in the susceptible strains: (i) glutathione transferase (*15*), (ii) the epoxide hydrolase selective for *trans*-epoxides and typically cytosolic in mammals (*16*), and (iii) the typically membrane-bound epoxide hydrolase that hydrolyzes *cis*-epoxides (*17*). Together, these enzymes can effectively detoxify lipophilic epoxides by generating excretable