transported in segregated rate classes, each with a distinctive composition, supports the structural hypothesis of axonal transport. Furthermore, these observations are part of a growing body of data that indicate that the biologically relevant units of axonal transport are likely to be cytological structures and not individual protein molecules.

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Changes in Sediment Storage in the Coon Creek Basin, Driftless Area, Wisconsin, 1853 to 1975

Abstract. *For any time period, total basin sediment yield can be used to make reliable estimates of upland erosion rates only when no significant change in sediment storage is in progress. In the case of Coon Creek, almost 50 percent of human-induced sediment has historically gone into floodplain storage and less than 7 percent has left the basin. However, some of the stored sediment is becoming mobile, and the present yield per unit area may actually be increasing downstream with the augmentation coming from the storage loss.*

Sediment yield is much less sensitive than change of sediment storage as an indicator of environmental change in some highly impacted stream basins (*1*). Because of these storage changes, there may be a poor correlation between material supplied to the stream by upland erosion and sediment yield at the lower end of the basin. These findings reinforce conclusions drawn from earlier research in the southeastern United States (*2*).

A sediment budget was constructed for Coon Creek, a drainage basin of 360 km^2 in the Driftless Area of southwestern Wisconsin for two periods: 1853 to 1938 and 1938 to 1975 (Fig. 1). Investigators measured the storage of modern sediment (since 1853) during the period 1974 through 1979, using techniques described in (*3*). Most storage is along streams, with alluvial deposits in the main valley accounting for about 75 percent of all measured sediment in the basin.

The sediment yield of Coon Creek since the beginning of agricultural activity was estimated on the basis of reservoir sedimentation rates from the nearby, physically and agriculturally similar Beaver Creek Basin. The reservoir on Beaver Creek was built in 1867, and total sediment accumulation was measured in 1939 (*4*) and in 1976–1977. The accumulation for both time periods was adjusted by means of the Brune trap efficiency curve (*5*) to estimate sediment inflow.

Total sheet and rill erosion since 1853 was estimated by applying the universal soil loss equation (*6*, *7*) at different dates and integrating the rates. Upland gully erosion was estimated by subtracting, during the period of peak erosion and sedimentation, the sum of the rates of upland sheet and rill erosion and the measured tributary erosion (*3*) from the sum of the rates of storage gain and sediment yield. This estimate is a minimal value: gully erosion was probably a greater proportion of the total erosion than indicated in Fig. 1. The overall average depth of erosion for 1853 to 1975 is 13.2 cm and compares well with 9.3 cm from an earlier estimate (*8*), which was based on soil-profile truncations and on consideration of sheet erosion on open pasture and cultivated land. Had woodland and gully erosion been included, the two estimates would have been closer.

Colluvium is the residual after the sum of storage gain and sediment yield is subtracted from total erosion. It is the least reliably quantified component of the sediment budget.

The most significant pattern to emerge from this sediment budget is that sediment yield has been small compared with either erosion or change in sediment storage. In view of the fact that so much emphasis has been placed on sediment yield as an indicator of erosional processes (*2*), it is instructive to realize that in this area sediment yield was only about 6 percent of all upland erosion

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estimated to have occurred between 1853 and 1938 and only 11 percent of the net sediment accretion in stream valleys.

In order to estimate short-term sedimentation rates, differential rates of sediment accretion were estimated by reconstructing stream and valley deposition rates at several sites in the main valley (as, for example, that illustrated in Fig. 2). A composite of these estimates shows that accretion increased from negligible rates at the time of European settlement to a peak of over 3000 × 10^6 g km^{-2} of drainage area per year in the 1930's. These peak estimates were substantiated by sediment deposition rates measured in several small reservoirs and debris dams (*9*). Floodplains at that time were aggrading at a rate of about 15 cm $year^{-1}$. At the same time, sediment yield was only about 160 × 10^6 g km^{-2} $year^{-1}$, about 5 percent of the storage gain.

Soil conservation measures of the 1930's and thereafter severely curtailed upland erosion (*7*). Net storage rates for the present cannot yet be measured to adequate precision, but analysis of ten subbasins indicated that, for the period from 1962 to 1975, sediment delivered from the upland to stream channels and floodplains was only about 55 × 10^6 g km^{-2} $year^{-1}$ (*7*), and this places an upper limit on the net gain in alluvial storage. At the same time, considerable stream-channel and bank erosion is occurring with net loss of alluvium at many surveyed valley cross sections. Present sediment yield has not been measured from the Coon Creek Basin, but yields from comparable basins in the region range from 50 to 200 × 10^6 g km^{-2} $year^{-1}$. If this range is applicable to Coon Creek, sediment is now more likely to leave than to enter valley bottom storage, and there appears to be net loss of storage. Thus, in the short term, sediment yields may be deceptive indicators of upland erosional processes.

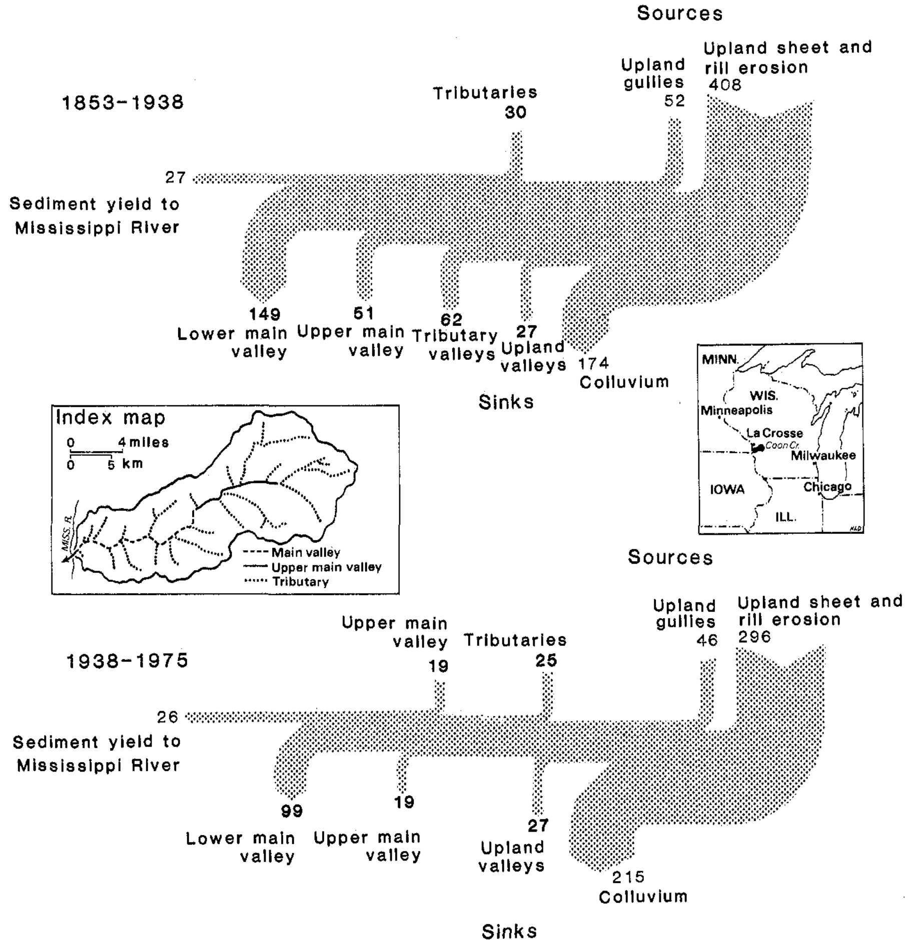

Fig. 1. Sediment budgets for Coon Creek, Wisconsin, 1853 to 1938 and 1938 to 1975. The basin is about 25 km southeast of La Crosse, Wisconsin, and has an area of 360 km^2. Numbers are annual averages for the periods in 10^3 m^3 $year^{-1}$. Bold numbers are measured; other numbers are estimated. The upper main valley, which was a sink for sediment in the earlier period, has become a partial source of sediment in the later period.

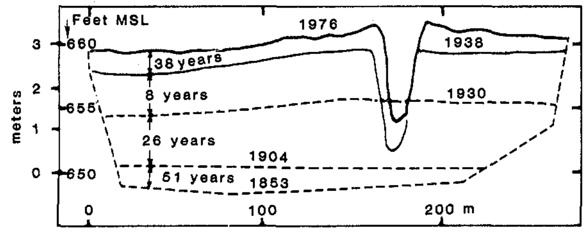

Fig. 2. A cross-sectional profile in the lower main valley of Coon Creek showing succeeding, higher floodplain levels dated from 1853 to 1976; *MSL*, mean sea level. Such accretion accounts for most storage in the Coon Creek Basin.

Limited evidence indicates that sediment yields from large basins (> 300 km^2) in the Driftless Area have changed relatively little over the past 50 years (*10*). At the same time, there has been a significant decrease in the rates of upland erosion and valley accretion. This finding suggests that the correlation between upland erosion and sediment yield is poor in highly disturbed basins where relatively large changes of storage are occurring. The present widely held concept is that sediment yield per unit area decreases with basin size (*11*), whereas the data from Coon Creek suggest that sediment yield per unit area may begin to increase with basin size in this and, by inference, in other agriculturally disturbed basins in humid regions. The data also strongly suggest that yield per unit area at a point in the system can change with time as a result of changes in sediment storage. If these inferences are correct, present concepts of the relation of drainage area to sediment yields will need to be rethought and further investigation is necessary.

Changes of sediment storage have qualitative as well as quantitative significance. Many agricultural and industrial chemicals, such as pesticides and polychlorinated biphenyls, adsorb on soil particles, and stream sediment measurements have been an important technique in monitoring the movement of these pollutants (*12*). Losses from or gains to storage would give deceptive measures of environmental impact from a given land or waste treatment. For example, a recently applied pollutant may disappear into storage, giving anomalously low concentrations farther downstream. Moreover, storage of long-lived chemicals attached to sediment particles may pose a long-term pollution problem.

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Merkel Cell Receptors: Structure and Transducer Function

Abstract. *An electron microscopic and electrophysiological investigation was made of Merkel cell–neurite complexes in the sinus hair follicles of the cat. These mechanoreceptors respond with very precise phase locking to high-frequency vibratory stimuli as well as to static hair displacements. The mechanoelectric transduction process is faster than that known for any other somatic mechanoreceptor. These data show that the nerve endings themselves and not the Merkel cells are the mechanoelectric transducer elements in these receptors.*

The structure and function of Merkel cells (MC's), which occur in association with a distinct type of mechanoreceptor in vertebrate skin, have been debated ever since Merkel first described the cells in 1875 (*1*). In mammals MC's are most abundant in the epidermal touch corpuscles and in the external root sheath of sinus hairs (vibrissae) (*2–4*). In both places MC's are contacted by nerve endings to form slowly adapting mechanoreceptors. These complexes have similar response properties in all mammalian species so far investigated (*5*). However, it is not known whether MC's are the mechanosensitive transducer elements of the receptor (*6*). On the basis of ultrastructural evidence, it was suggested that MC's could be secondary sensory cells (*3, 4*). Since the cytoplasm of MC's is rich in dense-core granules, it was assumed that mechanical deformation of the MC's would cause the generation of a receptor potential, which would be transmitted to the nerve endings through the release of a chemical transmitter from the dense-core granules at specialized zones of contact between the MC's and the nerve endings. However, since the nerve endings morphologically resemble those in other types of mechanoreceptors, a second possibility is that the mechanoelectric transduction process may take place at the nerve endings and not at the MC's (*3*).

Electrophysiological investigations have supported both these hypotheses. In newborn kittens afferent responses were recorded from touch corpuscles before the MC's had differentiated (*7*), and it was concluded that the nerve endings were the mechanoelectric transducer elements. In contrast, Horch *et al.* (*8*), who studied the discharge and excitability characteristics of afferent responses elicited from touch corpuscles, concluded that the action potentials were generated through a synaptic mechanism. They considered the MC's to be the receptor elements, and this interpretation is now generally accepted, even though it conflicts with several other findings. For instance, MC's survive denervation unaltered for several months (*9*), which is unusual for secondary sensory cells (*10*). Identification of a transmitter substance in the dense-core granules has long been unsuccessful, and the supposed synaptic transmission has not been blocked (*4, 6, 11*). Recently, however, a "Met-enkephalin–like" substance was demonstrated histochemically in MC's (*12*), and this finding, together with an ultrastructural verification of "synapses" between MC's and nerve endings, suggested anew that MC's function as receptor cells (*13*). We obtained new evidence against this concept by performing an electron microscopic and electrophysiological reinvestigation of the mechanoreceptors in the sinus hair follicle of the cat.

A cat was perfused with 2.5 percent phosphate-buffered glutaraldehyde and several sinus hair follicles were removed, embedded in Araldite, and cut transversally or longitudinally in serial semithin or ultrathin sections. Examination with an electron microscope confirmed previous observations concerning the ultrastructure of MC-neurite complexes (*2, 3, 14*), but in our view the morphological details suggest that their function is quite different from that of sensory cells. The MC's are situated in a regular manner in the external root sheath and are far more numerous—about 3000 were counted even in small sinus hair follicles—than has been suggested. Only 50 to 70 percent of them contact a nerve terminal, which then always lies on that side of the MC which is directed toward the follicle's orifice. If the MC's have a receptor function, not so many would lack a nerve contact.

The distribution of dense-core granules in the cytoplasm of MC's is always alike, whether a nerve contact exists or not. The dense-core granules are most numerous in that part of the MC's which might also be contacted by the nerve endings; usually they are concentrated in the peripheral cytoplasm and often outside the zone of contact with the nerve terminal (Fig. 1A). Thus the distribution of dense-core granules in the MC's appears to be independent of the presence of a nerve ending and inappropriate for the disposition and release of a transmitter substance. Such release is supposed to take place at "synapse-like" membrane contacts between MC's and nerve endings (*3, 4, 6, 13*). These specialized zones are situated mostly at the periphery of the disklike nerve terminals, but can be found with (Fig. 1B) and without (Fig. 1C) dense-core granules at the presumptive presynaptic side. Thus a specific affinity between the zones of contact and dense-core granules is not apparent. Also, for the operation of a synaptic mechanism in a receptor that can sustain a 1200-Hz discharge, many more dense-core granules would have to accumulate at the supposed transmitter release sites than are generally visible.

The synapse-like structures may, in fact, be desmosome-like attachment points between MC's and nerve endings. [The historical interpretation is understandable in view of the difficulty in distinguishing between true synaptic and merely adhesive cell contacts (*15*).] The MC's thus may function not as sensory cells but as abutments for the deforma-

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