cells lacking Tpo1 show increased expression of enzymes that are involved in producing lysine, one of the amino acids used as building blocks to make proteins. This finding led the authors to speculate that polyamine export might be involved in protecting cells against oxidative stress.

Removing the carboxyl group (COOH) from lysine — that is, decarboxylation of lysine — produces a polyamine called cadaverine. Although yeast cells have not previously been reported to produce cadaverine, they make another polyamine, putrescine, by decarboxylating the amino acid ornithine[4]. Putrescine is a precursor molecule that is needed to make the polyamines spermidine and spermine, which activate a quality-control process called autophagy in which cell components are degraded and recycled[5]; therefore, putrescine is also crucial for protecting cells against stress.

Lysine and ornithine have very similar molecular structures, and the authors found that Spe1, the enzyme that decarboxylates ornithine, can also decarboxylate lysine to generate cadaverine. Although experiments with purified Spe1 revealed that the enzyme has a much lower affinity for lysine than it does for ornithine, Olin-Sandoval *et al.* showed that yeast cells can take up lysine from the surrounding culture medium to increase its concentration inside the cell, such that Spe1 will then convert it to cadaverine. Thus, harvested lysine is decarboxylated to cadaverine, which, in turn, is exported from the cell by Tpo1 (Fig. 1). Although the production of cadaverine by Spe1 was accompanied by increased production of putrescine, the levels of spermidine and spermine were not affected, suggesting that lysine uptake and cadaverine production do not affect autophagy.

The increase in lysine levels in the yeast cells that harvest the amino acid from outside the cell might elicit feedback mechanisms to inhibit lysine production. In yeast cells, the generation of lysine from the amino acid aspartate requires NADPH (Fig. 1). Therefore, the harvesting of lysine from outside the cell results in NADPH being spared from use in the production of lysine. Using mathematical modelling of cellular metabolism, the authors found that decreases in the production of lysine would result in an attenuated flux of molecules through the oxidative part of the pentose phosphate pathway — the metabolic pathway that is the dominant source of NADPH. Thus, harvesting high levels of lysine enables stressed cells to produce more NADPH through the pentose phosphate pathway to deal with accumulated ROS. Consistent with this, the authors found that lysine-harvesting cells were less sensitive to the oxidative-stress agent diamide than were cells that did not harvest lysine.

Supplementation of methionine, another amino acid whose synthesis requires large amounts of NADPH, also improves the tolerance of cells to diamide[6]. But Olin-Sandoval and colleagues found that lysine harvesting is even better than methionine supplementation at improving diamide tolerance. Furthermore, cells that harvested lysine showed less ROS accumulation than did cells that did not harvest lysine. Whether cadaverine (and putrescine) improves the tolerance of cells to stress, in addition to the other effects of lysine harvesting on metabolism, remains unclear.

Many metabolic processes are conserved in evolution between yeast and mammalian cells, and yeast is a widely used model organism for studying human cells[7]. The authors therefore also evaluated whether lysine harvesting is a general mechanism for improving stress tolerance, and indeed found this to be the case in several other species of yeast, as well as in *Bacillus subtilis*, a species of the Gram-positive group of bacteria. However, although the authors demonstrated that several different human cell lines can harvest lysine, lysine harvesting did not make these cells more tolerant to oxidative stress. This is probably because human cells cannot synthesize lysine themselves, and therefore do not need a supply of NADPH to support biosynthesis of lysine; in these cells, harvesting lysine would not free up the capacity to create NADPH.

"Lysine-harvesting cells were less sensitive to oxidative stress than cells that did not harvest lysine."

Despite the lack of protective effects of lysine harvesting in human cells, the findings are still exciting because they provide an excellent demonstration of how apparently unrelated metabolic pathways interact. Moreover, they illustrate how a seemingly simple process — that is, the harvesting and decarboxylation of lysine — can drive major metabolic reprogramming that leads to an increase in the cell's capacity for producing NADPH. Besides these general findings, the study is also relevant for efforts to use yeast as a cell-factory system, because oxidative stress presents major problems for many production processes in such cell factories[7]. The findings of this study indicate that supplementing yeast-cell medium with lysine could help the cells to overcome this stress, and thus improve the efficiency of production of various valuable chemicals. ■

Jens Nielsen *is at the BioInnovation Institute, DK2200 Copenhagen N, Denmark; the Department of Biology and Biological Engineering, Chalmers University of Technology, Gothenburg, Sweden; and the Novo Nordisk Foundation Center for Biosustainability, Technical University of Denmark, Kongens Lyngby, Denmark.*
e-mail: nielsenj@chalmers.se

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HYDROLOGY

Groundwater resilience in sub-Saharan Africa

An analysis of aquifer replenishment in sub-Saharan Africa shows that reduced precipitation does not always deplete groundwater reserves, challenging the idea that these reserves will decrease in response to global warming. SEE LETTER P.230

RICHARD W. HEALY

The population of sub-Saharan Africa is currently about 1 billion, and is predicted to double by 2050 (go.nature.com/2zj9kca), whereas the region's climate is predicted to become drier during the same period[1]. Clearly, the demand for fresh water will increase. Whether groundwater can satisfy this demand is a looming question. Little is known about the rates at which water is replenished to groundwater aquifers[2,3] in that region, and thus the rate of sustainable withdrawal. On page 230, Cuthbert *et al.*[4] identify the processes involved, and examine the long-term trends of aquifer replenishment in sub-Saharan Africa. The authors conclude that future drying climatic trends could affect surface-water supplies, but might not decrease groundwater supplies.

Aquifer replenishment occurs naturally in two general forms: precipitation that infiltrates at the land surface and percolates to the water table (most common in humid regions), and infiltration from streams and other surface-water bodies (most common in arid regions).

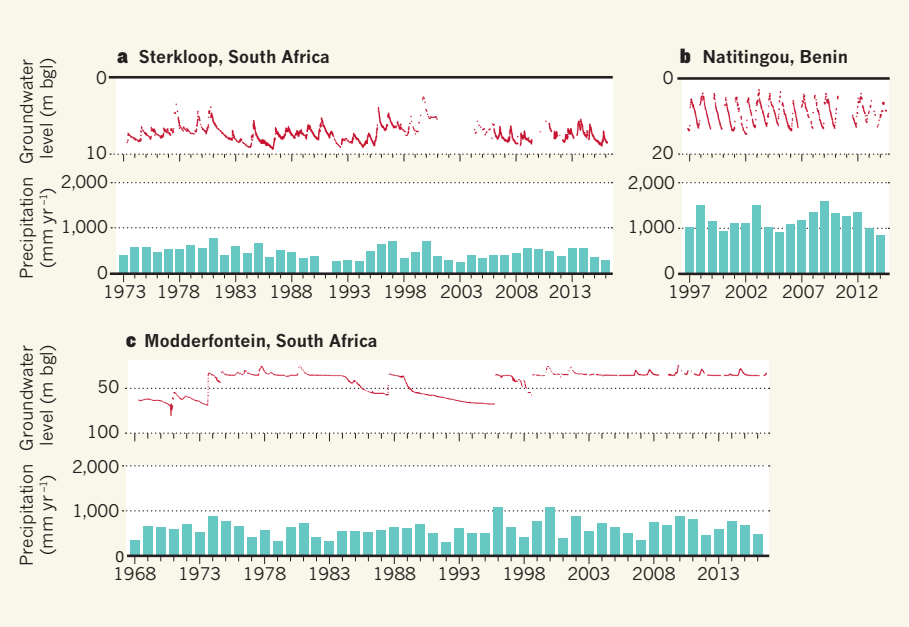

Figure 1 | Groundwater levels and annual precipitation at sites in sub-Saharan Africa. Cuthbert *et al.*[4] report multi-year data for groundwater levels (reported as metres below ground level; m bgl) measured at 14 wells across sub-Saharan Africa, and compare them with annual precipitation (millimetres per year) to see how aquifer replenishment corresponds with precipitation patterns. **a**, At some sites, such as Sterkloop in South Africa, annual rises and falls in groundwater levels synchronize with precipitation amounts. No precipitation data are available for 1991. **b**, At other sites, including Natitingou in Benin, the annual rise and fall of groundwater levels is the same from year to year, and is independent of the amount of precipitation. **c**, A third type of pattern, such as at Modderfontein in South Africa, is for multiyear periods of declining water levels interspersed with sporadic replenishments associated with intense precipitation events, with no apparent annual pattern of rising and falling levels.

Rates of aquifer replenishment are difficult to determine for various reasons, including a lack of data, high variability in the spacing and timing of replenishment, and uncertainty in estimation methods[3,5].

Groundwater levels monitored over time provide one measure of the volume of aquifer storage and rate of replenishment — rising groundwater levels generally imply that aquifers are being replenished. Unfortunately, there is a dearth of long-term groundwater-level data in sub-Saharan Africa[2]. Cuthbert and colleagues' study was made possible by the compilation of a rigorously reviewed, multi-decadal data set of water levels from 14 wells in areas across the region that are relatively unaffected by human activity. This unique data set allowed the authors to reach conclusions that have not been possible previously.

The authors calculated the ratio of annual replenishment to precipitation at the different sites, and thereby identified three types of aquifer response to precipitation. For the first type (Fig. 1a), replenishment increased almost linearly with increasing annual precipitation — a common trend in southern Africa[6]. Nine wells displayed this pattern. In this scenario, a minimum amount (threshold) of precipitation must fall before replenishment occurs. Drying climatic trends might lead to reduced rates of replenishment at sites characterized by this pattern of behaviour.

For the second type of aquifer response (Fig. 1b), annual replenishment was fairly constant from year to year, regardless of the amount of precipitation. This type of response is known as self-regulating behaviour[7], and Cuthbert *et al.* observed it in two wells in humid settings. Drying climatic trends at these sites will probably not alter replenishment rates.

The third aquifer-response type (Fig. 1c) showed little correlation between annual replenishment and precipitation, and was observed in three wells in semi- to hyper-arid settings. Replenishment was episodic, perhaps occurring only once every few years, mostly as a result of intense storms that occurred even in years of low total precipitation. The effects of climate change on replenishment rates for this response type are difficult to predict. Although total annual precipitation is predicted to decrease in response to global warming in most regions of sub-Saharan Africa, precipitation intensity is predicted to increase[1], so replenishment rates could also conceivably increase for aquifers of this type.

These results demonstrate a limitation of regional-scale assessments of the effects of climate change on groundwater resources, such as those published by the Intergovernmental Panel on Climate Change[1]. The large spatial scale of the climate-model predictions used in such assessments precludes a consideration of the variability and intensity of precipitation at the smaller scales that control aquifer replenishment in some environments. Cuthbert and colleagues' findings thus call into question previous conclusions, such as that "climate change is projected to reduce renewable surface water and groundwater resources significantly in most dry subtropical regions"[1].

The new findings also highlight the need for improvements in models of climate and hydrology. Climate models that can better predict the variability and intensity of precipitation events at the local scale, as well as the large scale, would allow hydrological models to better represent replenishment processes. Moreover, hydrology models that can account for local variability in geology, soils, land use and other features are also needed to enhance our understanding of where, when and how aquifer replenishment occurs.

Although climate models and hydrological models will continue to be key tools for evaluating water resources in sub-Saharan Africa, the importance of actual measurements of groundwater levels cannot be overstated. In this respect, Cuthbert and colleagues' compilation of long-term data from 14 wells is a valuable contribution, but the sparseness of this data set becomes clear when one considers the size of the region (approximately 23 million square kilometres). Measured groundwater levels are essential for estimating the amounts of water stored in aquifers and rates of aquifer replenishment; for identifying trends associated with climate, water- or land-use change; and for verifying the results of computational simulations of hydrologic models[8]. The monitoring of groundwater levels in sub-Saharan Africa must therefore be expanded to improve the understanding and management of groundwater resources at community, regional and country scales.

Better models and an expanded groundwater-level monitoring network should improve assessments of water resources in sub-Saharan Africa, but climate change is only one of several factors that must be considered. Human activities can have profound effects on groundwater quantity and quality, and how these activities will play out in the future is difficult to predict. For example, groundwater storage might increase as a consequence of land-use change, such as the replacement of native vegetation with pasture or row crops. But agricultural, industrial and mining activities, for example, might adversely affect groundwater quality, and thus limit the use of groundwater resources. Assessing the future availability of such resources in sub-Saharan Africa remains a difficult task, but Cuthbert and co-workers' study is a crucial step in the right direction. ■

Richard W. Healy *is at the US Geological Survey, Lakewood, Colorado 80225, USA.*
e-mail: rwhealy@usgs.gov

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ECOLOGY

Global maps of soil nematode worms

Accurate estimates of the biodiversity of soil animals are essential for conservation efforts and to understand the animals' role in carbon cycles. Such information is now available on a global scale for nematode worms. SEE ARTICLE P.194

NICO EISENHAUER & CARLOS A. GUERRA

Climate change is affecting biodiversity and the functioning of ecosystems around the globe[1]. Soil organisms are a crucial component of terrestrial biodiversity, and aid human well-being by making contributions in areas such as food security, water purification and carbon storage[2,3]. However, there is uncertainty about how the dynamics of soil biodiversity will change in the future as a result of agricultural intensification and alterations in climate and land use[4]. This is alarming, given the substantial gaps in current knowledge about the global distribution of soil biodiversity[5,6]. Large, worldwide data sets of soil microorganisms and fungi are available, and these have been generated using DNA-based approaches[7,8]. However, no quantitative assessment of soil animals has been undertaken at the global scale. On page 194, van den Hoogen *et al.*[9] now fill this gap by presenting the most comprehensive data set of soil-dwelling nematode worms reported so far.

Nematode worms are tiny (no more than 10 millimetres in length), transparent roundworms that live in films of water in the soil[10] (Fig. 1). They provide a useful subject for studying soil biodiversity because they are so common — their numbers can often exceed 1 million individuals per square metre of soil[11]. Nematodes represent approximately 80% of all the multicellular animals on Earth[11,12], and they have major roles in many ecosystems. In some cases, they have a negative effect, for example some nematodes are plant pests that can cause devastating losses to global crop yields. By contrast, other types can boost plant growth by driving nutrient cycling[10,12].

Van den Hoogen and colleagues assembled data on 6,759 soil samples taken from the top-soil layer of various ecosystems and all continents. The authors analysed the data to determine the numbers and types of nematode present (using microscopy, these groupings were made on the basis of the type of food eaten by a particular nematode, such as plants or fungi[10,11]). Soil nematode communities vary widely over small spatial scales, and this makes it difficult to use observations taken from a particular place to estimate the global nematode population. To overcome this problem, the authors used a machine-learning approach to analyse published and unpublished data to predict global nematode patterns and thereby generate global-level maps of nematode abundance and biomass. The authors estimate that 4.4×10^{20} nematodes inhabit the upper soil layer around the world, an incredibly large number that is comparable in scale to the estimated number of stars in the observable Universe.

"So far, soil animals have been neglected in carbon models."

Biodiversity for vertebrates, invertebrates and plants decreases from the Equator to the poles, and many possible mechanisms underlying this trend have been discussed[13]. By contrast, van den Hoogen and colleagues report the opposite pattern for nematodes: the highest abundance and biomass — indicators of biodiversity — occur in boreal forests (such as conifer forests in snowy landscapes) and tundra regions (cold plains that lack tree growth). This discovery thus challenges the current textbook view of the global distribution pattern of animal diversity. Instead, the authors' data suggest that the global distribution patterns of soil animals are more similar to those of soil-dwelling microbes[6,7].

Van den Hoogen and colleagues also present global estimates of the amount of carbon stored in nematode bodies, as well as estimates of nematode metabolic activity. The authors' projections indicate that nematode

50 Years Ago

The steam engine may be dead, but for Emmett connoisseurs there is always the wasp mistblower. This is one possible solution to the problem of getting rid of wasps from tall trees, designed by Drake and Fletcher Ltd … for spraying insecticides to high levels, and tested as part of a research programme by the Forestry Commission. A special "coconut outlet", originally used for palm trees, injects the spray liquid into an air blast. Other methods investigated include rotating sprinklers attached to the tops of individual trees, and a mobile sprinkler which reaches suitable heights with a telescopic mast. Only the mistblower, which is mounted on a tractor, seems feasible for large-scale applications — the respective disadvantages of the other two are a dearth of skilled climbers to install the machinery, and a time-consuming erection process for each operation.
From *Nature* 9 August 1969

100 Years Ago

While collecting information on the use of colour-protection among birds, my attention has been directed to … a very interesting generalisation, viz. that among birds which nest on the moors, seashores, and similar open places, (1) those which have the habit of remaining on their nests when danger threatens generally wear camouflaged uniforms, but their eggs seldom show any signs of colour-protection; while (2) those which are very shy and leave their eggs readily are generally conspicuously coloured, but their eggs are usually camouflaged. Amongst the first class are capercailzie, … wild duck, and bittern; and amongst the shy ones with camouflaged eggs are lapwing, … ring plover, and golden plover.
From *Nature* 7 August 1919