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Authors
Grant, Stanley B
Saphores, Jean-Daniel
Feldman, David L
et al.

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REVIEW

Taking the "Waste" Out of "Wastewater" for Human Water Security and Ecosystem Sustainability

Stanley B. Grant,[1,2]* Jean-Daniel Saphores,[1,3] David L. Feldman,[3] Andrew J. Hamilton,[4] Tim D. Fletcher,[5] Perran L. M. Cook,[6] Michael Stewardson,[2] Brett F. Sanders,[1] Lisa A. Levin,[7] Richard F. Ambrose,[8] Ana Deletic,[9] Rebekah Brown,[10] Sunny C. Jiang,[1] Diego Rosso,[1] William J. Cooper,[1] Ivan Marusic[11]

Humans create vast quantities of wastewater through inefficiencies and poor management of water systems. The wasting of water poses sustainability challenges, depletes energy reserves, and undermines human water security and ecosystem health. Here we review emerging approaches for reusing wastewater and minimizing its generation. These complementary options make the most of scarce freshwater resources, serve the varying water needs of both developed and developing countries, and confer a variety of environmental benefits. Their widespread adoption will require changing how freshwater is sourced, used, managed, and priced.

More than 4 billion people live in parts of the world where freshwater scarcity directly threatens human water security or river biodiversity (*1*). Threats to human water security can be overcome by building centralized infrastructure that harvests, stores, treats, and transports water for agricultural, industrial, and municipal uses. For countries that can afford it, this approach has greatly benefited human health and economic development, but it is often energy-intensive and comes at a steep ecological price. In the developing world, on the other hand, an estimated 1 billion people lack access to safe affordable drinking water, 2.7 billion lack access to sanitation, and many millions die each year from preventable waterborne diseases (*2*). Thus, developed and developing countries face separate but overlapping challenges. In developed countries, existing water infrastructure needs reengineering to sustain a high standard of living while reducing its environmental footprint and sustaining or restoring biodiversity. In developing countries, affordable infrastructure is needed to satisfy the water needs of humans and to preserve aquatic ecosystems (*1*). Meeting these twin challenges will require striking a balance between delivering new sources of water and using water more productively through pricing, conservation, and wastewater reuse.

[1]Department of Civil and Environmental Engineering, E4130 Engineering Gateway, University of California, Irvine, CA 92697-2175, USA. [2]Department of Infrastructure Engineering, Melbourne School of Engineering, Engineering Block D, University of Melbourne, Parkville 3010, Victoria, Australia. [3]Department of Planning, Policy, and Design, 202 Social Ecology I, University of California, Irvine, CA 92697-7075, USA. [4]Department of Agriculture and Food Systems, University of Melbourne, 940 Dookie-Nalinga Road, Dookie College, Victoria 3647, Australia. [5]Melbourne School of Land and Environment, University of Melbourne, Burnley Campus, 500 Yarra Boulevard, Richmond, Victoria 3121, Australia. [6]Water Studies Centre, School of Chemistry, Monash University, Victoria 3800, Australia. [7]Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, La Jolla, CA 92093-0218, USA. [8]Environmental Science and Engineering Program, University of California, Los Angeles, CA 90095-1772, USA. [9]Monash Water for Liveability, Department of Civil Engineering, Building 60, Monash University, Victoria 3800, Australia. [10]Monash Water for Liveability, School of Geography and Environmental Science, Monash University, Clayton, Victoria 3800, Australia. [11]Department of Mechanical Engineering, Melbourne School of Engineering, Engineering Block E, University of Melbourne, Parkville 3010, Victoria, Australia.

*To whom correspondence should be addressed. E-mail: sbgrant@uci.edu

How Is Water Used and Wasted?

Water use can be classified as consumptive or nonconsumptive, depending on how readily the used water can be reused. Consumptive use converts water into a form that cannot be reused. A portion of the water used for irrigation, for example, is evaporated, transpired, and incorporated into plant biomass. This consumed water is unavailable for reuse in the watershed over time scales of practical interest. In contrast, after nonconsumptive use, water can be captured, treated, and reused. If a nonconsumptive use degrades the quality of the water (for example, by adding contaminants), it is said to generate wastewater. An example of nonconsumptive use is the flushing of a toilet, which converts drinking water into domestic wastewater. In principle, domestic wastewater can be collected, treated to remove human pathogens and other contaminants, and then reused for potable or nonpotable purposes. Globally, the largest consumptive use of water is for agriculture, whereas the largest nonconsumptive use of water is for industrial and municipal supplies (*3*).

What Is Water Productivity and How Can It Be Improved?

Addressing threats to human water security and biodiversity will require getting the most out of locally available water resources. But what does that mean in practice? One way to evaluate water use is to consider its "productivity," defined as the value of goods and services produced per unit of water used. By improving water productivity, communities can enjoy the same goods and services, generate less wastewater, and leave more freshwater in streams, rivers, lakes, and coastal estuaries to support biodiversity. Because less water is harvested, treated, and transported, fossil fuel consumption and greenhouse gas emissions are reduced. Although water productivity has steadily improved in the United States since the mid-1970s, additional gains are possible both here and around the world (*4*). In this Review, we focus on three general strategies for improving water productivity (Fig. 1): substituting higher-quality water with lower-quality water where appropriate, regenerating higher-quality water from lower-quality water by treatment, and reducing the volume of higher-quality water used to generate goods and services.

What Are the Opportunities for Substituting?

Many municipal, industrial, and agricultural uses can be satisfied by lower-quality water. For example, treated domestic wastewater that would not be suitable for municipal water supplies may be perfectly suitable for industrial cooling and landscape irrigation, to name a few (*5*). Although the use of treated wastewater in the United States is currently limited (<5% of municipal supply), it could be expanded to 17 teraliters per year (Tl year^{-1}) (~27% of municipal supply), providing a new drought-resistant source of water in coastal areas where treated wastewater is currently discharged to the sea (*6*). Large-scale (centralized) wastewater treatment and potable substitution schemes can reduce overall energy consumption and reduce greenhouse gas emissions. In southern California, substituting potable water with treated wastewater consumes less energy and generates fewer greenhouse gases as compared to interbasin transfers of water or desalination of seawater or brackish groundwater (*7*).

Treated domestic wastewater is not the only lower-quality water that can be exploited in potable substitution schemes. Hong Kong's dual water system, which has been in operation for over 50 years, supplies seawater for toilet flushing to 80% of its 7 million residents, cutting municipal water use in the city by 20% (*8*). A triple-water distribution system at Hong Kong's International Airport, consisting of freshwater, seawater, and treated graywater from sinks and aircraft washdown, cuts municipal water use by over 50% (*8*).

Potable substitution can also be implemented at neighborhood and single-home scales (Fig. 2). Rainwater (from roofs) and graywater (from laundry, dishwashing, and bathing) can be used in place of drinking water for a variety of activities. The reuse of graywater for toilet flushing and yard irrigation can cut household municipal water use by 50% or more (*9*). The energy cost, water savings, and reliability associated with rainwater harvesting depend on engineering considerations (e.g., contributing roof area and storage tank volume), local climate, connected end uses (e.g., toilet, laundry, and hot water), and temporal patterns (*10*). In a case study of a model home in Melbourne, Australia, the use of rainwater tanks to supply water for laundry, dishwashing, toilets, and an outside garden reduced household municipal water use by 40% (*9*). However, even in Melbourne, where rainwater-harvesting schemes are commonplace, they contribute a modest 5 gigaliters (Gl) year^{-1} to the city's overall water budget, which represents 1.2% of the city's total water use and 1.4% of its municipal supply (*11*).

Stormwater runoff from roads and other impermeable surfaces is another locally available source of water, but here the challenge is harvesting and storing the runoff (which can be generated over very short periods of time) and adequately removing contaminants (pathogens, metals, and organic pollutants). These challenges can be overcome through the integration of natural treatment systems into the urban landscape, including green roofs, rain gardens, biofilters, and constructed wetlands (*12*). Processes responsible for pollutant removal in natural treatment systems include (*12*–*15*) gravitational sedimentation of large particles, pathogen removal by solar ultraviolet (UV) inactivation and predation, filtration of colloidal contaminants, oxidation of labile organics by hydrolysis and sunlight-generated reactive oxygen species, precipitation of metals, and nitrogen removal by bacterially mediated nitrification and denitrification in sediments. Plants play a key role, taking up excess nutrients and serving as both a source of organic carbon to fuel denitrification, and a source of oxygen through their root systems to fuel nitrification. As runoff moves through natural treatment systems, a portion of the water returns to the atmosphere (evapotranspiration); a portion infiltrates into the subsurface (groundwater recharge); and the rest can be harvested, stored, and ultimately used for nonpotable purposes. In Melbourne, stormwater harvesting is a relatively minor component (5 Gl year^{-1} or 1.4% of municipal water use) of the city's water budget (*11*), but including stormwater reuse schemes in new greenfield and brownfield developments until 2050 could result in a sevenfold increase in nonpotable water availability for the city (35 Gl year^{-1} or 9.8% of municipal water use) (*16*).

Integrating natural treatment systems into urban landscapes confers many benefits beyond improving human water security. In warmer climates, the evapotranspiration of runoff moderates the urban heat island effect (*17*), whereas infiltration recharges the groundwater and provides environmental water for local wetlands and riparian zones (*12*). The construction of new wetlands or reinvigoration of existing wetlands creates habitats for resident and migratory species and sustains biodiversity by enhancing habitat heterogeneity, connectivity, and food web support (*18*). When storm water is locally detained and retained throughout the catchment, less runoff enters rivers and streams, pollutant loads are reduced, and flow regimes more closely resemble predevelopment conditions (*19*). As a result, streams are less likely to overtop their banks and cause flooding (*20*), and the negative effects of urbanization on stream health and function, collectively known as the "urban stream syndrome" (*21*), can be mitigated (*22*).

What Are the Opportunities for Regeneration?

With adequate treatment, higher-quality water can be regenerated from wastewater. Because additional goods and services are produced every time a parcel of water is recycled, regeneration has the potential to significantly increase water productivity. A prime example of regeneration is potable reuse, in which wastewater is treated with conventional and advanced methods and then added back to the water supply either directly (direct potable reuse) or indirectly, by holding the water for a time in groundwater or surface-water reservoirs (indirect potable reuse) (*5*, *6*).

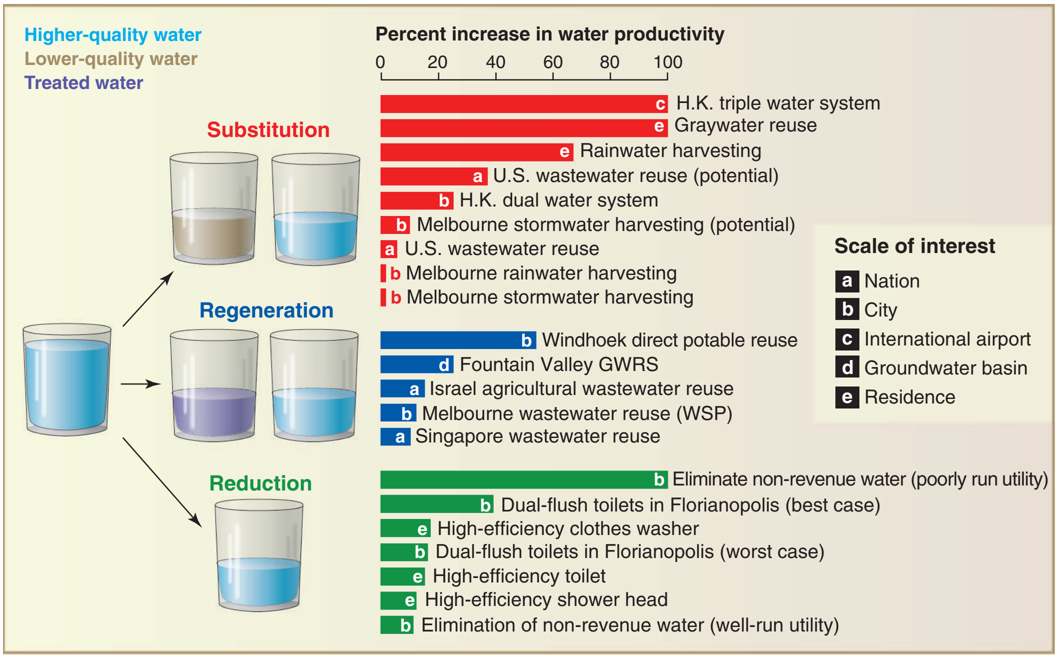

Fig. 1. (**Left**) Three complementary approaches for improving the productivity of higher-quality water. The water level in each glass shows how much water is used in producing a fixed value of goods and services. Substitution uses lower-quality water in place of higher-quality water for some activities. Regeneration transforms lower-quality water into higher-quality water by treatment. Reduction achieves the same value of goods and services using less higher-quality water. In these hypothetical examples, each option cuts by half the use of higher-quality water and therefore doubles its productivity. (**Right**) Percent increase in water productivity associated with the 21 case studies described in the text (*51*). These productivity improvements are illustrative only and will vary substantially in practice. The scale at which a particular water-saving intervention was implemented is indicated. The bars are color-coded to match the three general approaches for improving water productivity.

Apart from a few small-scale facilities, direct potable reuse is not practiced in the United States. However, several indirect potable reuse facilities are operational. The world's largest is the Groundwater Replenishment System (GWRS) in Fountain Valley, California, which treats up to 97 Gl year^{-1} of domestic wastewater using conventional (primary and secondary sewage treatment) and advanced (microfiltration, reverse osmosis, and UV disinfection) techniques (*23*). Water produced by the GWRS provides approximately 20% of the water needed to maintain the local groundwater aquifer in Orange County, a primary source of municipal supply for more than 2 million residents.

Internationally, the longest-running example of direct potable reuse is in Windhoek, Namibia, where recycled wastewater (mostly domestic sewage) has been added to the potable water distribution system more or less continuously since the late 1960s with no obvious adverse health effects among the population of several hundred thousand (*24*). The current facility produces enough water (7.7 Gl year^{-1}) to meet approximately 35% of the city's municipal water needs.

Among the centralized options for augmenting potable water supplies, potable reuse is preferable to interbasin water transfers for several reasons (*25*): (i) Interbasin water transfers reduce the water available at the source for critical ecosystems and agricultural production; (ii) transporting water over long distances can be energy- and carbon-footprint–intensive; and (iii) the water transmission systems are vulnerable to disruption by natural and human-made disasters, such as earthquakes and acts of terrorism. All three problems are evident in California, where the southern part of the state has long relied on water imported from sources located hundreds of kilometers to the east and north. In 2001, an estimated 4% of the electric power consumption in California was used for water supply and treatment (largely transportation) for urban and agricultural users; this estimate increases to 7% if end uses in agriculture (which are mainly related to pumping) are included (*26*). The depletion of source waters in the state has led to habitat deterioration, the decline and extinction of native fish species, the near-collapse of the Sacramento–San Joaquin River Delta ecosystem (*27*), and the desiccation of Owens Lake, whose dry lake bed is arguably the single largest source of asthma- and cancer-inducing respirable suspended particles in the United States (*28*). Potable reuse also has advantages relative to the desalination of seawater. By one estimate, potable reuse consumes less than one-half the energy [~1000 to 1500 kilowatt-hours per megaliter (kWh Ml^{-1})] beyond conventional treatment) required for the desalination of seawater (~3400 to 4000 kWh Ml^{-1}) (*25*).

Relative to the classification scheme presented in Fig. 1, some nonpotable wastewater reuse is best described as regeneration, provided that the treated effluent replaces water of equal or lower quality, such as river diversions (Fig. 2). For example, 73% of Israel's municipal sewage is treated and reused for agricultural irrigation, which is equal to roughly 5% of the country's total water use (*29*) and 13% of its municipal supply. In Singapore, 27 Gl year^{-1} of highly treated domestic wastewater is used primarily for industrial applications, which is equal to 5% of its total water use and 9% of its municipal supply (*30*).

Relatively low-energy centralized approaches for nonpotable wastewater reuse are also available, such as waste stabilization ponds (WSPs), in which sewage is directed through a series of open-air shallow ponds where physical processes (flocculation and gravitational sedimentation), microbial processes (algal growth, aerobic and anaerobic heterotrophic metabolism, nitrification, and denitrification), and exposure to sunlight jointly remove pathogens, organic contaminants, and nitrogen (*31*). Effluent from WSPs can irrigate crops (Fig. 2) or recharge groundwater aquifers, and the ponds themselves may provide a much needed quasi-wetland habitat for waterbird conservation (*18*). The world's largest WSP system, the Western Treatment Plant in Melbourne, produces 40 Gl year^{-1} of treated wastewater, equivalent to 11%

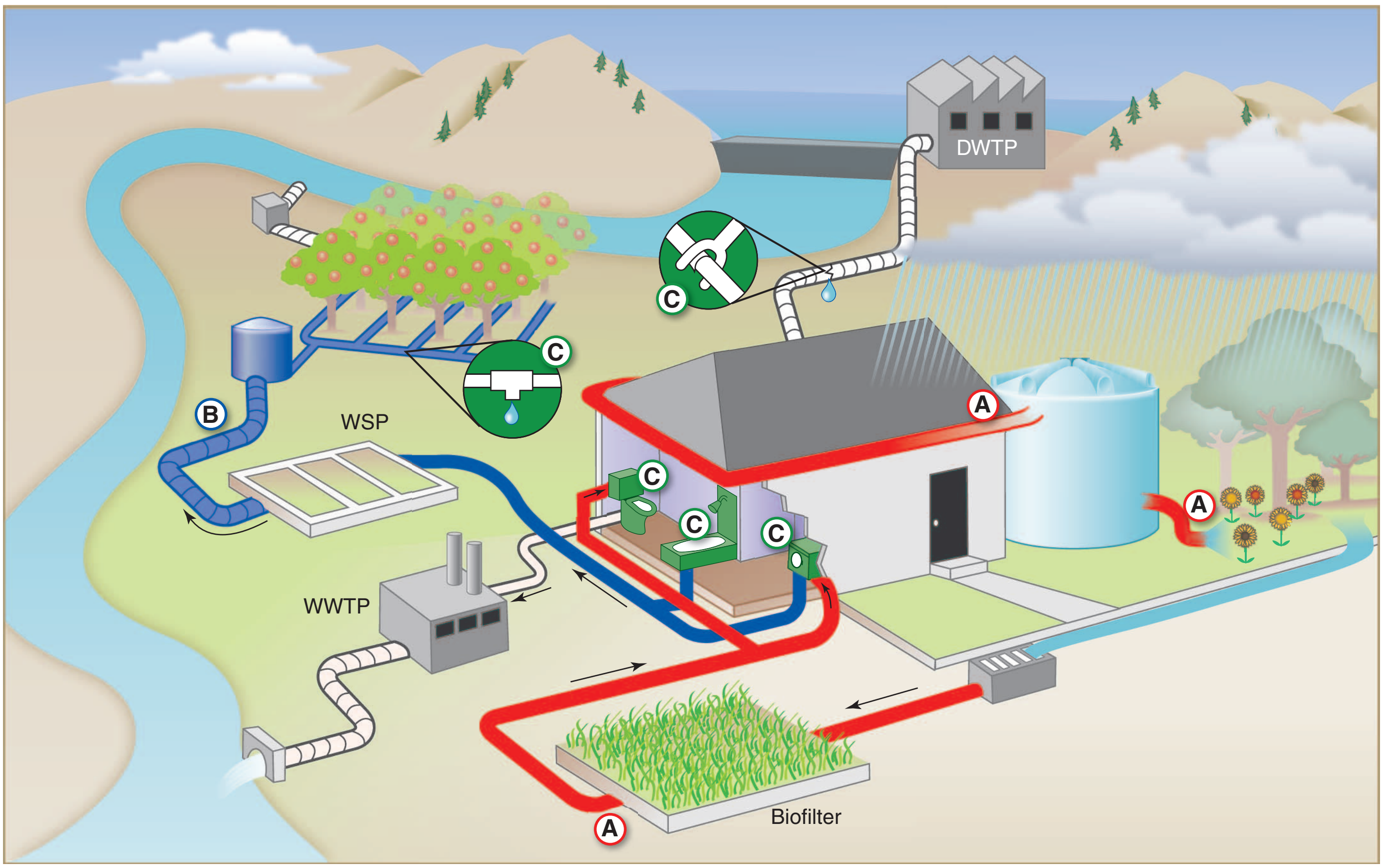

Fig. 2. Practical examples of substitution (**A**), regeneration (**B**), and reduction (**C**) at the household scale. Substitution includes watering a garden with rainwater from a rainwater tank and flushing toilets and washing laundry with treated stormwater effluent from a biofilter. For regeneration, a waste stabilization pond (WSP) transforms sewage from the house into high-quality water used for irrigating an orchard. Reduction includes repairing leaks in the water distribution system, drip irrigation, a dual-flush toilet, a low-flow shower rose, and a front-loading clothes washer. Other water infrastructure elements shown include a conventional drinking water plant (DWTP); a conventional wastewater treatment plant (WWTP); and a river diversion (supplying the orchard).

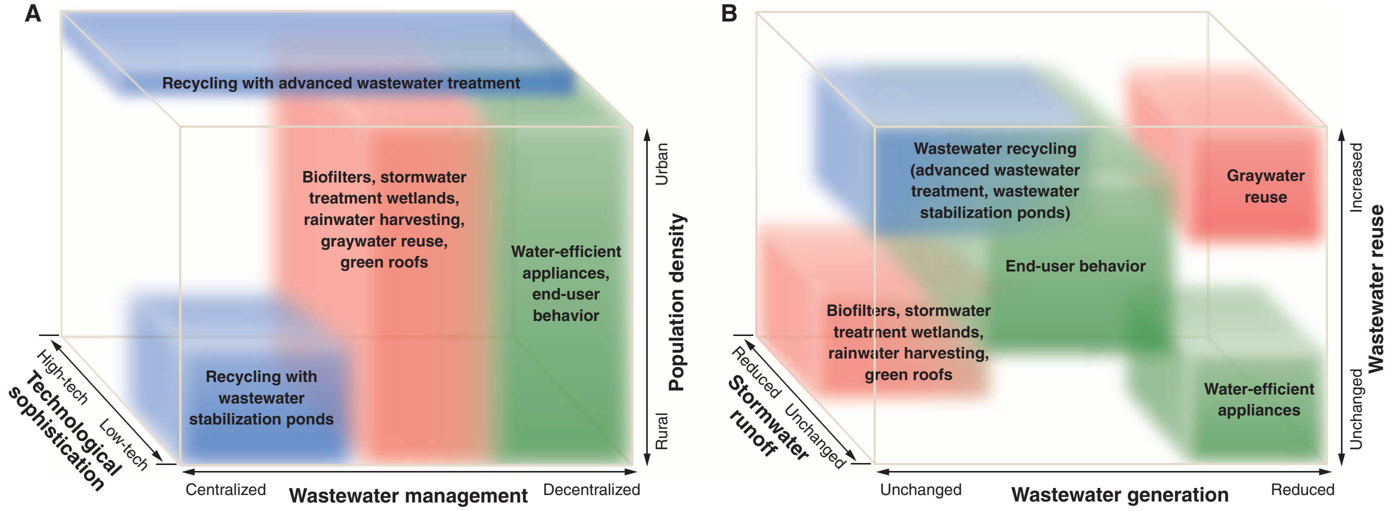

Fig. 3. Wastewater reuse and water-saving schemes discussed in the text, arrayed relative to a few key attributes (**A**) and performance indicators (**B**). The color scheme matches that in Fig. 1; substituting, red; regenerating, blue; and reducing, green. Certain schemes can be classified in more than one way; for example, wastewater recycling with wastewater stabilization ponds might be considered blue or red, depending on the end use and what water is being substituted or regenerated. The adoption of water-saving schemes is influenced by policy, law, regulations, markets, and incentives.

of Melbourne's municipal supply, and uses approximately 500 kWh Ml^{-1} less energy than conventional wastewater treatment (*32*). Recycled water from the Western Treatment Plant is used for a variety of nonpotable applications, including in-plant uses and dual pipe schemes for the irrigation of agricultural crops, gardens, golf courses, and conservation areas.

Primary concerns associated with wastewater reuse include the buildup of contaminants and salts in soils (in the case of wastewater irrigation) and the possibility that incomplete removal of chemical or microbiological hazards during treatment may cause disease in an exposed population (*6*). Disease risk can be evaluated on a case-by-case basis using a statistical framework, such as quantitative microbial risk assessment, that predicts a population's disease burden, given the types and concentrations of pathogens that are likely to be present in the water, as well as particular exposure scenarios (*33*).

What Are the Opportunities for Reduction?

Water productivity can also be improved by reducing the volume of water used to produce a fixed value of goods and services. A modeling study of the water supply system in Florianopolis, Brazil, concluded that replacing single-flush toilets with dual-flush toilets would reduce municipal water use in the city by 14 to 28% and reduce energy use at upstream (drinking water) and downstream (wastewater) treatment plants by 4 GWh year^{-1}—enough energy to supply 1000 additional households (*34*). An analysis of 96 owner-occupied single-family homes in California, Washington, and Florida concluded that the installation of high-efficiency showerheads, toilets, and clothes washers reduced household use of municipal water by 10.9, 13.3, and 14.5%, respectively (*35*). Because water is not technically required for bathroom waste disposal, the installation of composting toilets and waterless urinals can reduce municipal water use even further (*36*).

Agriculture accounts for the majority of global freshwater withdrawals (*37*), and thus even small improvements in water productivity in this sector can result in substantial water savings. Water savings can be achieved by switching to less–water-consuming crops, laser-leveling of fields, reducing nonproductive evaporation of water from soil or supply canals, changing irrigation scheduling, and adopting more efficient sprinkler systems, including microirrigation techniques (drip irrigation and microsprinklers) that precisely deliver water to plant roots (*37*). These approaches could help mitigate escalating water demand associated with growing energy crops, such as corn, particularly if projected increases in U.S. biofuel production are realized (*38*).

Drinking water is lost after it leaves treatment plants because of physical leaks in urban water distribution systems and poor accounting. Worldwide, the total volume of this "nonrevenue water" is estimated to be 49 Tl per year (*39*). Pipeline losses range from over 50% in much of the developing world to less than 10% in well-run utilities (*39*). The World Bank estimates that if just half of the losses in developing countries were eliminated, \$1.6 billion would be saved annually in production and pumping costs, and drinking water could be extended to an additional 90 million people without the need for new treatment facilities (*39*).

What Is the Role of Water Quality?

Protection of water quality is also a priority. The Catskill Mountains supply drinking water for New York City. When agriculture and residential developments threatened surface-water quality, the city considered building an \$8 billion water treatment plant, but instead opted to spend \$1 billion buying land and restoring habitat in the water supply catchment. This approach obviated the need for a treatment plant, saved the city billions of dollars in capital and ongoing operations and maintenance costs, and preserved a critical ecosystem (*40*).

What Is the Right Mix of Wastewater Reuse and Water-Saving Schemes?

The wastewater reuse and water-saving schemes described above are each tailored to a particular scale of implementation (from single homes to entire countries), population density (from urban to rural), and level of technological sophistication (from high-tech to low-tech) (Fig. 3A). Potable substitution schemes using advanced wastewater treatment may be feasible in an urban context, but not in a rural context. Furthermore, no single scheme simultaneously maximizes wastewater reuse, minimizes wastewater generation, and minimizes stormwater runoff (Fig. 3B). How does a community identify the right mix of schemes that will optimize their water systems? One study evaluated infrastructure options for a hypothetical residential development in the southeast of England, and concluded that every community has a technological state-of-the-art equilibrium beyond which tradeoffs are required (*41*). Wastewater reuse and water-saving schemes can improve water use, energy use, and land use up to the equilibrium point. Beyond the equilibrium point, further reductions in water use require increasing either energy use (if high-tech options are used) or land use (if low-tech options are used) (*41*). Human behavior should also be considered in the assessments of optimal water management strategies, as was done in an elegant systems modeling study of water supply options in Chennai, India (*42*).

Because end-user behavior affects all aspects of water and wastewater management (Fig. 3B), changing attitudes and expectations may be more effective than finding infrastructure solutions to water scarcity. Turf grass consumes upward of 75% of residential drinking water in arid and semi-arid areas of the United States (*43*). If water resources in this region continue to dwindle, reducing the volume of water used for yard irrigation (for example, by implementing advanced irrigation technologies) may not be sufficient. Homeowners may have no choice but to replace turf grass with xeric landscaping (*44*). Such wholesale rethinking of our relationship with water is an example of a "soft-path" approach to water management. As a general principle, the soft-path approach is characterized by (*4*, *45*) (i) viewing water as a service rather than an end in itself, (ii) adopting ecological sustainability as a fundamental criterion, (iii) matching the quality of water delivered to that needed by its use, (iv) planning from the future back to the present, and (v) ensuring community and citizen involvement in water management planning.

What Are the Main Roadblocks?

Efforts to improve water productivity will require overcoming economic, planning, regulatory, institutional, and public acceptance challenges. Key obstacles include uncertainty regarding the longevity and maintenance costs of infrastructure; upfront costs for piping, storage, and land; quantifying unpriced benefits; and overcoming water underpricing.

The first obstacle will probably resolve as experience is gained by vendors who develop wastewater-reuse and water-saving infrastructure, by community planning agencies that introduce them, and by municipal agencies or households that maintain them.

Underpricing of water is more serious because it leads to excess water demand and revenue shortfalls for water utilities. Underfunded utilities tend not to maintain infrastructure or repair leaks, adequately treat wastewater (spoiling scarce water resources), or extend service to the urban poor, who are then forced to buy expensive water from street vendors (*46*). Policies that inhibit full-cost pricing for water to ensure social equity or for other reasons may exacerbate this situation (*47*). When implemented in ways that ensure utility accountability to users and fair rate structures, full-cost pricing may help manage water resources sustainably and equitably (*48*), sending appropriate and realistic price signals that reflect the true cost (including externalities) of water use.

Many of the approaches discussed in this review require fundamental changes to the built environment, which can be promoted through a multi-objective approach that fosters collaboration with developers, a culture of innovation, and community implementation capacity (*49*). Distributed water infrastructure can be introduced as part of comprehensive planning strategies that promote compact urban forms with mixed land uses and a focus on urban amenities, encourage alternative forms of transportation to permit narrower streets and reduce demand for parking, foster energy saving and waste recycling, promote water savings, and reduce liability for innovative developers.

Regulatory changes are needed to promote water conservation by mandating water-efficient plumbing, fixtures, and appliances. Regulatory changes are also needed to provide a consistent risk-management framework for water recycling schemes. Australian water reuse regulations, for example, emphasize protecting human health, which may foster a more favorable regulatory environment than in the United States, where water laws emphasize environmental health (*6*).

Finally, lessons from wastewater recycling systems indicate that the adoption of new water infrastructure depends on public acceptance. Public support for wastewater reuse, for example, is higher for uses such as landscape irrigation or car washing that minimize human contact (*6*). Public acceptance is also a necessary condition for utilities to embrace wastewater reuse and for firms to incorporate it in their production processes, provided that recycling wastewater neither substantially increases their costs nor triggers additional regulatory scrutiny.

To increase the likelihood of public acceptance, decision-makers should first demonstrate why changes are required to avert water shortages and that these water-saving schemes are safe. In addition, concerted and sustained efforts must focus on properly maintaining water infrastructure, especially when it pertains to wastewater reuse; on allowing stakeholders to monitor the uses and operations of wastewater recycling; and on vigilantly ensuring the protection of public and environmental health (*50*). Overcoming obstacles to the widespread adoption of wastewater recycling and water-saving measures is a sine quo non for meeting the water challenges of the future.

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51. Water productivity P is defined as the value of goods and services V generated per unit of water used Q: $P = V/Q$. The percent change in potable water productivity associated with the implementation of a water-saving scheme is $\Delta\overline{P} \equiv 100(P_2 - P_1)/P_1$, where P_1 and P_2 represent the productivity of potable water before and after the scheme is implemented (not all water-saving schemes discussed in the text directly reduced potable water use, but for consistency across the 21 case studies, water savings were benchmarked relative to potable water use at the appropriate scale). Assuming that the water-saving scheme does not change the value of goods and services produced, $\Delta\overline{P}$ can be calculated directly from potable (municipal) water use before (Q_1) and after (Q_2) scheme implementation: $\Delta\overline{P} = 100(Q_1/Q_2 - 1)$.

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REVIEW

Conversion of Wastes into Bioelectricity and Chemicals by Using Microbial Electrochemical Technologies

Bruce E. Logan[1]* and Korneel Rabaey[2]

Waste biomass is a cheap and relatively abundant source of electrons for microbes capable of producing electrical current outside the cell. Rapidly developing microbial electrochemical technologies, such as microbial fuel cells, are part of a diverse platform of future sustainable energy and chemical production technologies. We review the key advances that will enable the use of exoelectrogenic microorganisms to generate biofuels, hydrogen gas, methane, and other valuable inorganic and organic chemicals. Moreover, we examine the key challenges for implementing these systems and compare them to similar renewable energy technologies. Although commercial development is already underway in several different applications, ranging from wastewater treatment to industrial chemical production, further research is needed regarding efficiency, scalability, system lifetimes, and reliability.

There is substantial energy in organic matter that is currently wasted or lost in treatment processes. Treatment of organic-rich wastewater currently consumes about 15 GW, or about 3% of all electrical power produced in the United States (*1*), but domestic, industrial, and animal wastewater together contain ~1.5×10^{11} kilowatt-hour (kWh) of potential energy (~17 GW of power) (*2*). Capturing part of this energy would provide a new source of electrical power that would also avoid the consumption of energy for wastewater treatment. Furthermore, agricultural practices could be modified to annually produce an additional 1.34 billion tons of biomass for energy production, without affecting food production (*3*), which is equivalent to more than 600 GW of continuous power. These different sources of waste organic matter can be a rich resource for energy production if we can develop cost-effective methods for harnessing this energy. Alternatively, we could capture this waste biomass energy in industrial processes to make other useful chemicals, such as biofuels or industrial chemicals, that currently require electricity or organic substrates for this purpose.

Recently developed microbial electrochemical technologies (METs) that use microorganisms to catalyze different electrochemical reactions, such as microbial fuel cells (MFCs) that generated electrical power, are promising approaches for capturing the energy in waste biomass for diverse purposes. Energy production by electrochemical processes or conventional combustion requires a fuel to provide electrons and an electron acceptor (oxidizer). In METs, organic matter is the fuel, and oxygen is the primary oxidizer for aerobic respiration by bacteria. However, many other soluble chemical species can serve as oxidizers for anaerobic bacteria, including nitrate, sulfate, and carbon dioxide. Bacteria known as exoelectrogens have the ability to transfer electrons outside the cell to insoluble electron acceptors, such as iron and other metal oxides, or to electrodes in bioelectrochemical systems. The most commonly studied microorganisms are various *Geobacter* and *Shewanella* spp., but many other bacteria have been found to possess exoelectrogenic abilities (*4*). Electrons are transferred by these bacteria outside the cell indirectly, by using electron shuttles such as flavins and phenazines (*5*–*7*), or directly by using outer membrane proteins (*8*). These mechanisms can occur in combination with self-produced conductive pili called nanowires (*9*, *10*). In contrast, electrotrophic microorganisms can directly or indirectly accept electrons into the cell (*11*).

[1]Department of Civil and Environmental Engineering, 212 Sackett Building, The Pennsylvania State University, University Park, PA 16802, USA. [2]Laboratory of Microbial Ecology and Technology (LabMET), Ghent University, Coupure Links 653, 9000 Ghent, Belgium, and Advanced Water Management Centre, The University of Queensland, Brisbane, QLD 4072, Australia.

*To whom correspondence should be addressed. E-mail: blogan@psu.edu

How Do Microorganisms Generate Electricity from Organic Matter?

The use of exoelectrogenic microorganisms in MFCs allows electrical power generation from nearly any source of biodegradable organic or inorganic matter in water that does not directly require oxygen as a part of the degradation process. These organic sources include simple molecules such as acetate, ethanol, glucose, and hydrogen gas; polymers such as polysaccharides, proteins, and cellulose; and many types of wastewaters from domestic, food processing, and animal sources (*12*, *13*) (Fig. 1). In an MFC, bacteria release electrons to the anode and protons into solution, resulting in a negative anode potential of about –0.2 V (versus a standard hydrogen electrode) that is generally only slightly more positive than that of the half-cell reaction for the substrate (e.g., a midpoint potential at pH = 7 of –0.28 V for acetate) (*14*). In most cases, oxygen in air is used as a sustainable oxidizer at the cathode, with a typical maximum potential of +0.3 V, producing an overall maximum cell potential of +0.5 V. Cathode potentials obtained in MFCs are considerably lower than theoretical values (~+0.8 V, with oxygen) even with Pt-catalyzed cathodes (*15*, *16*) (Fig. 1). One of the most promising nonprecious metal materials used for oxygen reduction in MFCs is activated carbon, because it is both inexpensive and renewably produced from waste biomass (*17*). Nitrate is an alternate electron acceptor that produces comparable cell voltages because of its high solubility relative to oxygen (*18*). Voltages cannot be increased by linking MFCs in series as is done with batteries (*19*, *20*). However, higher voltages can be captured from arrays of MFCs by wiring them to charge capacitors in parallel and then discharging the capacitors in series, resulting in nearly additive voltages from the individual MFCs (*21*).

The power densities produced by MFCs are lower than those possible by using hydrogen fuel cells because of high internal resistances, the limited temperature and solution conditions tolerated by microorganisms, substrate degradability, and biofilm kinetics. Hydrogen fuel cells use an ion-exchange membrane as a solid electrolyte for charge transfer. Membranes are not required in MFCs, and using a membrane between the anode and cathode can add internal resistance, which will