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quickly remobilized to other organs when needed. For example, energy to defend a plant against a detrimental environmental change can be supplied through rapid and efficient remobilization of stored carbohydrates. In species living in hostile environments, remobilization of carbohydrates is important when an unfavorable condition disappears and buds need to sprout again. In some plants, carbohydrates remobilized from roots are used to break plant dormancy after winter. For some tropical plants, for example, cassava, these carbohydrate reserves are also used for costly developmental processes, such as flowering or fruiting. Understanding the mechanisms through which carbohydrates can be mobilized to and remobilized from storage roots is a crucial question in storage root biology, as it could shed light on how organisms determine the production and allocation of energy resources to suit all energetic demands.

What are the model species to study plant storage roots? Despite the importance of storage roots for food security, to date there is no clear preferred model system to study them. This is partly because research on plants with storage roots has traditionally been restricted to a few species, and in many cases plants that develop storage roots have long life cycles and/or polyploid genomes. Major research efforts are being invested in cassava and, although several tools are available for this species, including the availability of a fully sequenced genome and advanced molecular tools such as genome editing, it has a long life cycle, which can make genetic approaches quite slow. Chicory, which is used as a crop in some countries, also develops storage roots and is easy to grow and to transform, and recent genomic advances now allow for state-of-the-art molecular analyses; however, its lengthy biennial life cycle may also present problems when performing genetic studies. Radish has recently emerged as a potential model system, given its diploid and relatively small genome, its relatively short life cycle (three months), the availability of bioinformatic tools, and robust protocols for genetic transformation. Whether or not all relevant aspects of storage root development and physiology can be studied with a single species will probably determine what becomes the preferred model system.

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Quick guide

Rain harvesting by plants

Matt Biddick[1,*] and John T. Van Stan II[2]

What is rain harvesting by plants? Plants must successfully navigate nature's water market to survive. Just as some cities economize water resources by more effectively managing stormwater, some plants have developed ways of economizing water supply by capturing rain with their canopies. For these plants, their canopy morphology helps them intercept disproportionately high amounts of rainwater relative to their less precipitation-adapted counterparts. This phenomenon is known as 'rain harvesting' and has been described in a myriad of plant taxa (Figure 1). Rain harvesting is distinct from rain interception. Almost all plants passively intercept precipitation to some extent; however, far fewer are known to have evolved specific adaptations to maximize their hydrological profits, although new examples are frequently described.

What kind of traits help plants harvest rainwater? Plants employ all kinds of traits to harvest rainwater. Arguably the most frequently observed are those seen in leaves. Many plants, particularly monocotyledons, produce strap leaves that are deeply channelled through the center (Figure 1), reminiscent of the rain gutters that adorn modern homes. Some plant leaves pair this gutter-like structure with a surface that repels water, forcing the rainwater to ball-up and roll into the channel. Another strategy is to use specialized leaf scales (like the trichome scales visible as dots in Figure 1, bottom right) to snatch water up before it drains off the leaf. Less observed, yet equally as functional, some plants produce stems with grooved surfaces that funnel the rivulets of water descending the trunk (known as 'stemflow'). These grooves maximize the amount of water flowing to the soil directly beneath the plant. This is economically advantageous in habitats where fresh water is scarce and for

Figure 1. Diverse rain-harvesting adaptations in plants.
Clockwise from top left: Specialized water storage tanks in bromeliads. Rain-gutter-like leaves in the Lord Howe Island screw pine (*Pandanus forstreri*, Australia). Deep grooves channel stemflow in the roots of the epiphytic *Griselinia lucida* (New Zealand). Leaves stippled with scales that this epiphytic fern, *Pleopeltis michauxiana* (Georgia, USA), uses to take up rainwater. Gutter-like, water-repellent leaves of *Tradescantia ohiensis* (Georgia, USA). Specialized absorptive tissue found at the end of *Pandanus forsteri* aerial roots.

plants with shallow root systems (such as some monocotyledons).

Why do plants harvest rainwater?
Plants harvest rainwater for a several reasons; however, rain-harvesting traits are most readily seen in plants that inhabit water-scarce environments where economizing water supply is most critical. For example, many rain harvesters are epiphytic and live in the canopy of their host trees. Epiphytes cannot utilize water stored in the forest floor and therefore lack a reliable water supply. Because they are suspended off the ground, their roots are also susceptible to desiccation and embolism. This makes the epiphytic lifestyle akin to living in the desert. It is perhaps no wonder then that epiphytic plants share many morphological adaptations with desert plants.

What if it does not rain? Some rain-harvesting taxa have evolved ingenious means of storing the water they harvest, making them less susceptible to the sporadic and unpredictable nature of rainfall events. For example, many orchids maintain a sheath of dry tissue surrounding their exposed roots that readily soaks up and stores water and the nutrients dissolved within. Some ferns, like the species with the leaf scales mentioned earlier, can dry up (almost) completely, then wait in a dormant state until the next storm comes. By contrast, bromeliads take a different approach and support pools of rainwater and organic debris known as 'phytotelmata'.

Is the rainwater economy fair?
If your definition of 'fair' includes equitable access to resources, then almost certainly not. The trickle-down economics of rainwater harvesting can leave much less precipitation for the 'little guys' in the understory. While the fall of rainwater over a landscape can be considered somewhat homogenous, the morphology of the plants comprising that landscape results in an overtly heterogeneous distribution of this valuable resource. For example, large canopy trees, which may already take a large share of soil resources, intercept greater amounts of rainwater relative to smaller subcanopy plants — not just because of their size. Should these trees also possess specialized rain-harvesting traits, the unequal distribution of rainwater is even further exacerbated. Some rainwater harvesting plants may take advantage of the large canopy trees, living epiphytically above the ground to gain access to a more abundant rainwater market. Though much remains to be quantified in this realm, the distribution of rainwater among individuals probably follows a Pareto-like distribution, much like how wealth is distributed in society.

What about mist, fog, or dew?
The leafy and woody traits that help plants harvest rainwater can also aid in harvesting mist, fog, or dew. Many epiphytic plants growing in cloud forests, for example, are well adapted to harvesting these atmospheric water sources. Branches and stems with channelled bark will also fill and flow with fog, mist, and dew. Many early naturalists and isolated communities noticed the harvesting of water by plants from atmospheric sources other than rain. Ancient naturalists, such as Theophrastus and Pliny the Elder, reported dew harvesting, and indigenous communities in the remote Canary Islands used mist and fog harvested by trees as a water supply.

Why does rain harvesting matter?
Harvesting rain, and other atmospheric waters, expands the opportunities for plants to live in diverse environments that may otherwise be inhospitable. Plants are a cornerstone in the building

of sustainable societies by providing the ecological foundation of our food system, stabilizing slopes and coastlines, yielding the raw materials to construct our very houses, and providing various other ecosystem services. In fact, rainwater intercepted by some plants is consumed by animals dwelling in the canopy. Koalas, for example, drink from the stemflow that descends *Eucalyptus* tree trunks. Thus, rain harvesting by plants also matters for the conservation of animal communities.

What is next? Despite being observed by Theophrastus more than 2,000 years ago, research into the interception and harvesting of rainwater by plants has only recently begun. As a result, research is needed on rain harvesting from various perspectives. From an evolutionary perspective, further study is needed to investigate where hotspots of rain-harvesting traits have evolved. From a biogeochemical perspective, we know little about the contribution that these sorts of traits have on the heterogeneous distribution of water (and the nutrients it carries) across vegetated landscapes. From a physiological perspective, it remains unclear the degree to which rain harvesting contributes to the overall water and nutrient uptake by many important crop plants, although we suspect it is greater than appreciated. Finally, from an ecological perspective, research is needed on how harvesting of atmospheric water by plants supports canopy-dwelling microbial and faunal communities.

Where can I find out more?

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Primer

Ribosome biogenesis and the cellular energy economy

David Shore[1,*] and Benjamin Albert[2]

Cell growth relies upon the ability to produce new proteins, which requires energy and chemical precursors, and an adequate supply of the molecular machines for protein synthesis — ribosomes. Although not widely appreciated, ribosomes are remarkably abundant in all cells. For example, in a rapidly growing yeast cell there are ~2–4 x 10^5 ribosomes, produced and exported to the cytoplasm at a rate of ~2,000–4,000 per minute, with ribosomal proteins making up ~50% of total cellular protein number and ~30% of cellular protein mass. Even in a typical human cell ribosomal proteins constitute ~4–6% of total protein mass, and ribosomes are present at ~10^7 per cell. We begin this primer by exploring the tight relationship between ribosome production and cell growth, which has important implications not just for the cell's global protein expression profile and maximum growth rate, but also for the molecular composition of the ribosome itself. We then discuss how and to what extent the expression of the RNA and protein components of ribosomes is fine-tuned to match the cell's needs and minimise waste. Finally, we highlight the importance of coordinated ribosomal RNA (rRNA) and ribosomal protein expression in eukaryotes and explore how defects in this process are associated with proteotoxicity and disease. A central underlying question addressed throughout is whether regulation of ribosome biogenesis has evolved to optimise energy efficiency or is instead (or in addition) driven by other goals, such as maximising cell growth rate, promoting adaptation to changing environmental conditions, or maintaining the stability of the cellular proteome.

Ribosomes: built for speed?

Individual ribosomes are large and complex assemblies, consisting of two independent subunits that each contain both rRNA and many small ribosomal proteins (Figure 1A). Although prokaryotic and eukaryotic cytoplasmic ribosomes differ in size, it is interesting to note that in both kingdoms rRNA dominates over ribosomal protein by mass, an unusual property for enzymes, which are generally composed mostly of protein. Furthermore, cytoplasmic ribosomes are invariably made up of a large number of small proteins (~55 in prokaryotes and ~80 in eukaryotes), the size of which falls within an unusually tight distribution when compared with protein size in other multiprotein complexes. In contrast, rRNAs are much less numerous and derived from either a single precursor transcript (in bacteria) or two transcripts (in eukaryotes).

Before considering the implications of ribosome biogenesis for the energy economy of the cell, it is worth asking why the ribosome is built the way it is. It has long been recognised that the abundance of ribosomes, which need to be duplicated every cell division, might itself place a limit on cell doubling time. A bacterial cell, for example, will not be able to duplicate any faster than the average time required for one ribosome to translate the complete set of ribosomal proteins (Figure 1B). Interestingly, a simple thought experiment suggests that this process might be accelerated if the total mass of ribosomal protein were divided into a relatively large number of small proteins, since nascent ribosomal proteins will not be able to participate in translation until their own translation is complete (Figure 1C). However, the production of many small ribosomal proteins requires more initiation events, which will sequester ribosomes from the elongation process, thus placing an upper limit on the optimal protein number for efficient ribosome autocatalysis. Based upon known translation elongation parameters in *Escherichia coli* and an estimate of the initiation penalty, it has been calculated that the optimal number of ribosomal proteins for maximum autocatalysis is very close to the actual number observed in *E. coli* (56 ribosomal proteins; Figure 1D). A similar logic has been applied to evaluate the burden of rRNA synthesis and the unusually tight size distribution of ribosomal proteins. The results of this analysis