



Plants as Teachers and Witnesses

One plant biologist reflects on seasonal re-pacing in a culture of constant action, as a gift learned from her study subjects.

Beronda L. Montgomery

Last winter, I visited McLeod Plantation Historic Site on James Island in South Carolina. When my family and I arrived at the McLeod site, the day was overcast and we could smell rain in the air. As we left the visitors center with the tour guide and rounded the path to the main entry of the plantation, my son and I broke off from the group as we all approached the “big house” directly in front of us, the gravel crunching on the dry, dusty ground beneath our feet. I looked at the abundant rain clouds and, although confident the dry grounds would eagerly soak up a downpour, I was concerned that the coming rain would lead us to a hurried exploration of the grounds, which I was most excited about, because this part of the plantation is where our enslaved ancestors would have spent the most time. In the face of rain, we would instead have to spend more time touring the house of the enslaver and former landowner. We entered the big house and followed the guided tour while keeping an eye on the sky each time we passed a window. As the tour came to an end, we were thrilled to see a small patch of blue at the edge of the storm clouds, and the rain held at bay.

As we began our journey through the grounds, constantly keeping an eye on the storm clouds, we glanced first at the restored original cotton gin to the left, and then our gazes lingered on a row of original houses that had served as the living quarters of the enslaved people to the right (*see page 40*). After a brief stop to peer into the gin that had processed countless pounds of cotton, we entered

one of the cabins, which were unbelievably small and desolate. The stillness of the air and the emptiness of the quarters were in stark contrast to the weighty and disconcerting feelings my son and I felt when we were inside.

As we stepped back outside the quarters, I was drawn to a massive tree directly ahead of us: the McLeod Oak. The tour guide said that it was believed to be upward of 600 years old. I reverently approached the tree and stood beneath its broad, sweeping branches and gently rustling leaves while my son ventured on. As the rain clouds began to fully dissipate in the distance, I stood under the oak tree, watching my son from a distance as he sat on a bench looking pensively over the cotton fields with the quarters behind him, quarters which had been built from local trees by the hands of the enslaved people themselves.

Standing under the McLeod Oak, I was awestruck by the realization that this living tree had stood in this same place at a time when what could have been our own enslaved ancestors inhabited and worked this land. Although our own familial roots were in the Arkansas Delta region, upward of 40 percent of enslaved Africans in the United States entered through Charleston, South Carolina. Thus, our ancestors had likely passed through this region, and it's possible distant relatives could have remained here.

This awareness weighed heavily in my thoughts and led me to question what this oak's life had been like, and what it had witnessed of the lives of the people living together with it on the McLeod land. I wondered

QUICK TAKE

Studying how trees adapt to the seasons teaches lessons about the importance of anticipation, appropriate response, and bearing witness. Humans likewise have seasonal shifts.

Modern humans' capacity for constant action and overworking can be balanced with season-informed, survival-enhancing behaviors, such as measured engagement in work and regular periods of rest.

For deciduous trees, spring demands a burst of action, summer requires focused productivity, fall is a transition in anticipation of rest, and winter is a time of pause. We must honor these natural cycles to thrive.

how its seasonal progressions might have annually marked time for these enslaved people. As I rested my hand on its substantial trunk, I pondered that not only had this oak shared the same time and place with our enslaved ancestors, but their exhalations in moments of weariness, bleakness, and even times of hope for better had directly supported its growth. This tree held their essence, bore witness to their lives, symbolized their tenacity, and lived on physically supported by the wood comprising a portion of its trunk, holding their transformed breaths. The McLeod Oak and other centuries-old trees stand as living witnesses to history as they persist on timescales much longer than human life.

Keepers of the Legacy

Plants, including the McLeod Oak with which I stood that day, carry evidence in their very beings of the lives of those with whom they have shared space. The carbon dioxide exhaled by animals and humans is inhaled by plants and, together with water and energy harvested from the Sun, is transformed first into sugars that sustain their lives and that build up their physical forms. Plants use these sugars to produce substances such as starch and cellulose, which in turn can be assembled into leaves and seeds, and also can be deposited into wood for trees.

Trees thus carry the very essence of humans, both past and present, in their bodies and bear witness to our existence. As humans, we are also dependent upon the oxygen that plants exhale, as well as many other gifts they offer to support our lives—fruits, nuts, seeds, wood, and shade. In standing with this tree, I also stood in the presence of ancestors.

Even though we were visiting in December, the McLeod Oak still bore green leaves because it is a Southern live oak tree (*Quercus virginiana*). Live oak trees are semideciduous evergreens that remain green throughout the year. However, in late winter or early spring, their new leaves emerge and push off the previous year's dying leaves, replacing them.

This oak reminded me of some of my very first work with plants as a burgeoning plant researcher in central Arkansas, when I investigated how light affects leaf color and development in deciduous Southern red oak trees (*Quercus falcata*). The Southern red oak is distinct from evergreen oaks in that it is deciduous and so responds to each season distinctly in easily observable ways: Spring finds Southern red oaks in anticipation and then a burst of action, summer marks a period of focused productivity, fall is a time when deciduous trees transition to a preparation for rest, and winter is a time of pause.

I stood wondering about what the McLeod Oak must look like in spring when its new,

bright green leaves emerge and its yellowing, older leaves wither and drop to the ground. I wondered how the pace and patterns of life of our enslaved ancestors must have changed across the seasons in parallel. Growing up in Little Rock, Arkansas, surrounded by the Southern red oaks that I later studied, I always anticipated the vast shadow cast when those trees were adorned with their many fully developed summer leaves, and the massive colorful pile of leaves they dropped in fall.

Unlike the seasonally varying cycles of plants, the current human condition, including my own, is too frequently a life of constant action. My biological knowledge of plants has grown over the years as I've studied their responses to changes in environmental cues such as light. So, too, has my appreciation for the many lessons I can learn from these organisms. Even the observational knowledge that I have gained from watching trees survive in the intensely hot, humid summers in the South of the United States, and now seeing these organisms survive brutally cold and snowy winters from my home in the North, has instilled in me a deep appreciation for how these

"In standing with this tree, I also stood in the presence of ancestors."

organisms anticipate and prepare for changes in temperature, light availability, and other environmental signals. The long days of summer are perceived as a sign to grow abundantly, whereas the shorter, colder days of winter signal a time for rest.

Studying how trees adapt to each season has taught me pointed life lessons—about the importance of anticipation, appropriate response, and bearing witness. Such lessons offer reflections on and applications for human "re-pacing" from constant action and our capacity for overworking, to season-informed and survival-enhancing behaviors, such as embracing measured engagement in work and regular periods of rest.

Springing into Action

I love spring. I am absolutely fascinated by the emergence of spring flowers and the annual budding of deciduous trees. Each spring, I eagerly look forward to those first few weeks of the season when I take a weekly walk along the same path in my neighborhood to mark the rapid changes in the flowers present and the new leaves emerging on deciduous trees. This year, in particular, in the wake of the coronavirus pandemic sweeping the globe, my walks were quieter, on nearly deserted sidewalks and streets. Yet this year, as always, spring found trees prepared to make



Illustrations by Stephanie Freese



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At the McLeod Plantation on James Island, South Carolina, the small quarters that were for the enslaved people stand near a large Southern live oak tree, the McLeod Oak (see page 38), purported to be 600 years old. The tree lived alongside these enslaved people, bearing witness to their lives. The carbon dioxide from their exhalations in times of weariness, bleakness, or hope for better supported the tree's growth.

a withdrawal from the bank of sugars carefully stored as starches in their roots. These plants anticipate spring as the time when these stores must be used to power their budburst and the subsequent emergence and growth of

"In spring, trees make a withdrawal from the bank of sugars carefully stored as starches in their roots."

new leaves. The arrival of new leaves is stimulated by the warmth and sometimes the extended period of sunlight that reliably marks the season. (See "Spring Budburst in a Changing Climate," March–April 2016.) This process has become a major focus of my studies. My research group has been exploring the light cues that plants use to perceive consistent changes in day length that shift with the seasons. Light cues also link to the processes of leaf development and greening that occur in spring.

I have spent more than two decades studying *phytochromes*, which are light-sensitive proteins that serve many purposes in plants, including the critical need to monitor and respond to *photoperiod*, the length of time that

a plant is exposed to light. Phytochromes measure hours of daylight versus darkness of night and confer photoperiod-dependent control over responses such as flowering and seed set. These proteins thus sense seasonal progression and accurately coordinate expression of key genes needed to match plant behaviors to a particular season. In spring, therefore, phytochromes coordinate gene expression associated with the production and growth of new leaves and flowers.

Southern red oak trees' newly emerged leaves, like those of many other trees, are vibrantly red in early spring. In my aforementioned studies with *Q. falcata*, I marveled at this early period of robust red pigment production in seedlings. These bright red pigments, called *anthocyanins*, may serve as sunscreen for the young leaves before they mature to the point of producing light-screening waxes and other compounds. These anthocyanins protect the leaves from absorbing too much light, which could result in damage during active development of the organelles that carry out photosynthesis. Failure to protect these important structures could lead to the plant overshooting how much light it needs to absorb for robust photosynthesis. In the absence of these red pigments, the leaves would suffer the equivalent of sunburn. Anthocyanins serve vital transient roles until other compounds protect maturing leaves. In addition, the anthocyanin pigments may deter herbivory by insects that are not as attracted to the color red as I am.

The new spring leaves result in plants entering a period of marked activity. Leaves are

like solar panels that harvest light for energy production. The harvested light energy, together with the uptake of animal- and human-exhaled carbon dioxide (CO₂), drives the production of sugars through photosynthesis, and the subsequent release of the byproduct, oxygen. This byproduct is essential for the animals and humans sharing the habitat with plants and, indeed, forms a return gift in a process of reciprocity for the CO₂ that plants receive.

Shortly after early spring, the McLeod Oak begins to flower, as do Southern red oaks (*right*) and other deciduous trees, although the process of continued flower development and maturation marks a transition to summer. The transition from red to green for young oak leaves is a vibrant seasonal marker of time as summer approaches. Since I began to study this process, I've frequently been reminded to reflect on the needed preparations for the shift of pace that lies ahead, when I transition from the end of an academic year in spring to different focal points for summer.

Summer of Productivity

Standing under the massive McLeod Oak last winter, I could vividly imagine the wide span of shade it must cast when fully adorned with its complete, mature summer foliage. Summer is a season when live oaks and deciduous trees such as Southern red oaks bear mature leaves. Because this phase does not encompass the mass emergence of new leaves, as is typical of spring, or the bulk loss of leaves for deciduous trees in fall, summer appeared to me when I was young to be a time when trees were just sitting there. As I began to learn more about plants, I learned summer was a time of intense, if hidden, activity. Apart from the generous offering of shade, a tree's busy summer life can be completely underestimated. Summer is when the broad and abundant green leaves are focused on energy production through photosynthesis.

Energy produced by leaves is used for processes that peak during summer, such as the production of new branches, the maintenance of other nonphotosynthesizing plant parts, and the important transition to reproduction. The reproductive phase is marked by the maturation of flowers, floral pollination, and the production of seeds that bear the next generation. Once these critical plant activities are taken care of, any excess energy can be stored in roots as starch or used for cellulose production. These latter processes restore energy banks that had been drawn upon in early spring, and they ultimately add to the wood of the tree, which represents a form of stockpiling "surplus" during a productive period, as well as storing the breath of animals and humans that contributed to the sugar-producing process of photosynthesis. In good environmental



Courtesy of Melody Rose

In early spring, the leaves of Southern red oak trees (*Quercus falcata*) are often red. Bright red pigments called *anthocyanins* serve as sunscreen for the young leaves until they are mature enough to produce light-screening waxes and other compounds. The long, dangling inflorescences also emerge in spring.

conditions that support higher levels or prolonged seasons of photosynthesis and growth, the surplus stored in wood results in wider tree rings than those produced in poor conditions. My enslaved ancestors' presence, thus,

"In summer, oak trees are busy as their mature leaves vigorously produce sugars and as they prepare for later seasons by storing surplus resources."

was "remembered" through the production of wood in this manner.

While I'm conducting research as a creative pursuit and my chosen profession, summer is likewise a busy period for me. During this period, we often expand the number of researchers engaged in our work as we host visiting summer students and are fully engaged in our research without simultaneously being involved in courses. The long days of summer are a period when the phytochromes that we study signal to plants the abundance of light for photosynthesis and energy production. Likewise, we frequently spend long days in the laboratory conducting experiments on plant responses to light to take full advantage of a time



uninterrupted by other school-year demands. We thus devote an abundance of energy to our research questions in summer. Our work is bolstered by the energy and enthusiasm of new researchers, as well as by the foundational knowledge and long-term vision of more experienced team members. Similarly, oak trees are robustly busy as the mature annual leaves vigorously produce sugars and as they prepare for later seasons by storing surplus resources.

As summer nears its end, as is characteristic for a deciduous tree, Southern red oaks begin to transition to more maintenance and preparation for a drop in activity as they perceive changes in seasonal cues that mark the arrival of fall.

Falling Toward a State of Rest

I enjoy fall as an adult, but that was not always the case. I remember fall more for the exhausting labor of raking leaves when I was a child than for the explosion of colors for

different means, the most obvious of which for some plants is dropping their leaves—the hallmark trait of deciduous plants. The shedding of leaves relieves the plant of a significant energy load, when maintaining these organs is no longer beneficial, because they are no longer active energy contributors.

Perennial plants instead put the limited energy produced in late fall into processes related to maintaining critical functions and key organs, such as buds and *meristematic tissues*—a type of tissue at the growing ends of stems and twigs that consists of undifferentiated stem cells, which can be stimulated to form distinct plant parts. Buds and meristems drive the formation of new tissues and organs throughout a plant's life cycle during times when they are actively needed and can be supported. Thus, fall is a time for reprioritizing energy allocations to those activities and behaviors that will ensure restorative rest and maintenance.

The shedding of leaves is not a haphazard or panic-based process on the part of plants, as the approach of winter is for me every year. Trees such as Southern red oaks drop their leaves in an orderly series of events by which they actively work to recover any nutrients that they can by recycling compounds such as green chlorophyll, the pigment for photosynthesis. I was fascinated the first time I learned that this recycling process is the key action that leads to fall colors, when leaves appear to turn yellow, orange, or red. These vibrant hues are indeed due to the colorful carotenoid and anthocyanin pigments that were synthesized in spring or throughout the life cycle of the trees and that become apparent as the plants' pools of green chlorophyll decline. (See "Why Leaves Turn Red," November–December 2002.)

We and other scientists have studied the finely orchestrated processes by which light-sensitive proteins perceive changes in day length to signal either the synthesis of chlorophylls, carotenoids, and anthocyanins in spring, or chlorophyll degradation in the shorter days in fall. Due to reduction in daylight hours, the phytochromes perceive the seasonal shift and coordinate expression of genes, including those producing the proteins that break down chlorophylls and promote *senescence*, or the aging and dropping, of leaves. This translation of seasonal cues to appropriate behaviors is one that always reminds me to prioritize staying in tune with my environment, such as preparing to adjust my activities and sleep during the shift to daylight savings time rather than powering through the change unacknowledged.

The leaves' falling, sometimes gracefully and always noticeably, marks the end of the autumn season. As the temperatures continue to decrease as winter approaches, plants

which I've come to eagerly anticipate the season. Fall is a flamboyantly colorful time—or at least ends as one. The cooler temperatures that emerge during fall, as well as a shortening day length, signal a time for plants to actively prepare for rest.

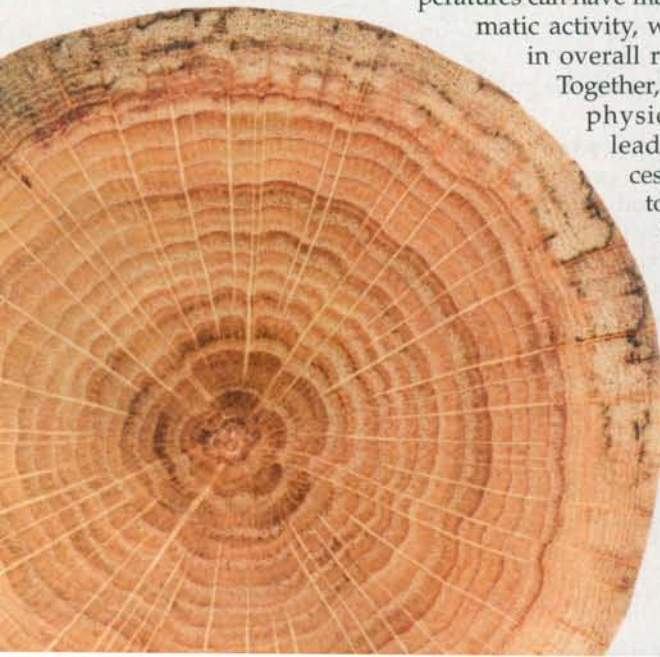
As a child, I never truly considered the meaning behind trees losing their leaves in fall. Only as I began to study biology as an undergraduate and to understand that inherited behaviors generally provide a benefit to organisms did I start to ask questions about plant behaviors associated with fall colors. The shorter days indicate reduced availability of light to drive photosynthesis. Additionally, cooler temperatures can have marked effects on enzymatic activity, which can also result in overall reduced metabolism.

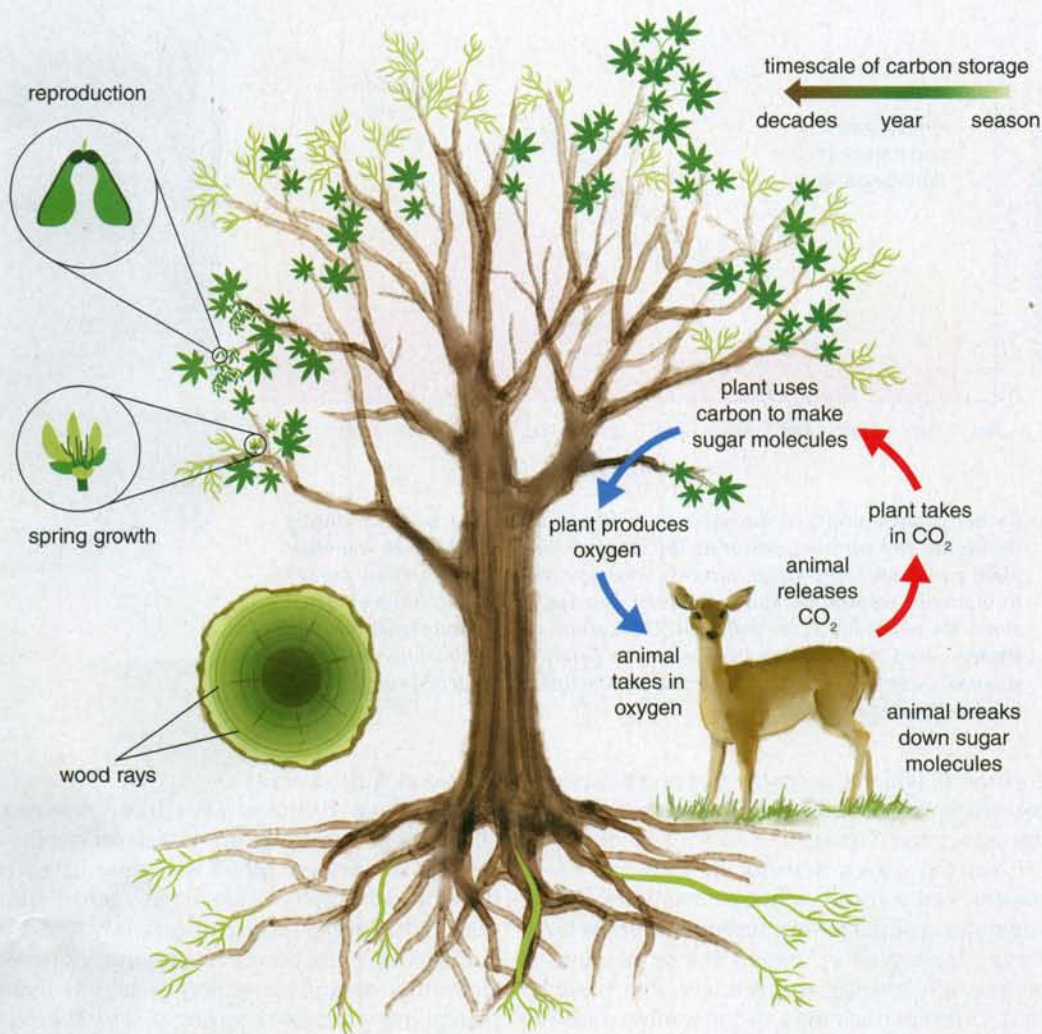
Together, these fall-associated physiological responses lead to molecular processes that plants need to reduce their energy burdens and actively initiate preparations to maintain essential functions through the pending winter.

Plants accomplish this transition toward a more restful period by many

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In good summer seasons that support high levels of photosynthesis for long periods, surplus carbohydrates are stored in the wood of Southern red oaks, resulting in wider tree rings than those produced in poorer years.





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proceed to hunker down for a period during which they largely cease activity and focus on maintenance or rest—a period of pause.

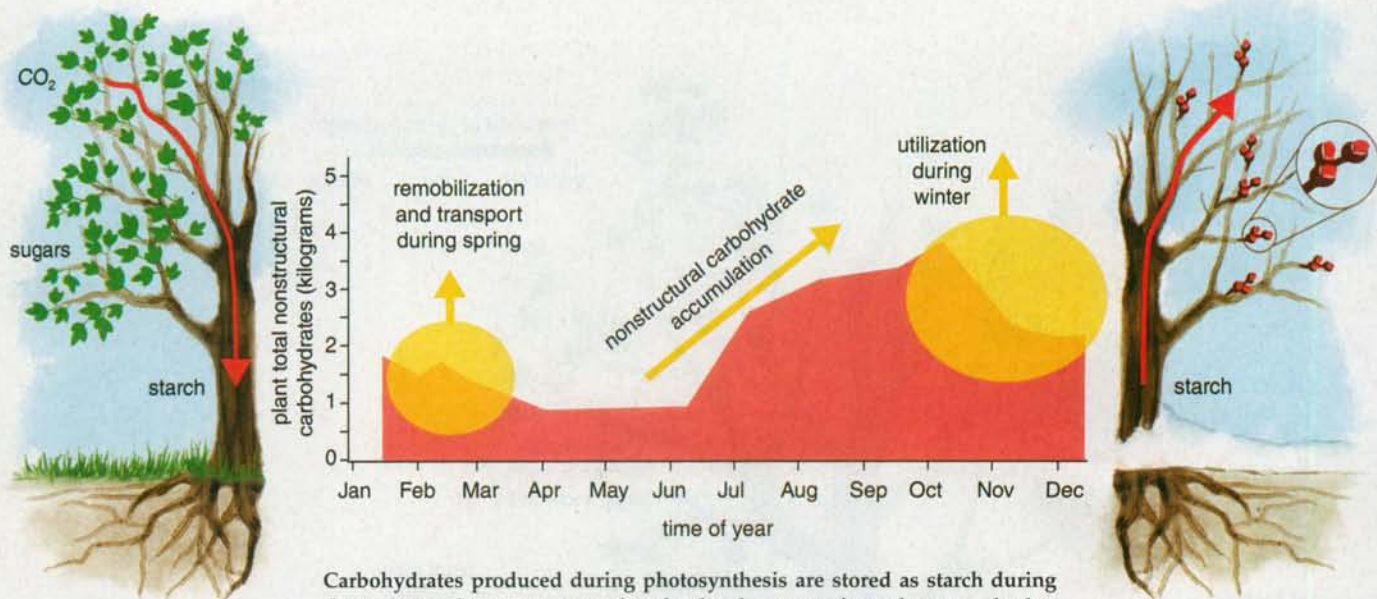
Winter as a Time of Pause

After many years of living in Michigan, I've learned to tolerate, if not enjoy, winter. For plants, the cold days and shortened daily periods of sunlight that typify winter offer limited opportunity for robust photosynthesis that would provide rich sources of energy for plant activity. Thus, plants—especially those that have sacrificed their leaves—have slower metabolism and diminished activity in winter. It is a time of planned pause by these organisms. Standing with the oak at the McLeod plantation, I wondered how my enslaved ancestors must have also used the annual dropping of the resident tree's leaves in the midst of winter, as is typical for live oaks, as a seasonal

sign that a slower period may have been upon them as well, due to the shorter hours of work with limited daylight hours.

During winter, when temperatures reach the freezing point, deciduous trees cease active water flow to avoid ice formation in the vascular tissues, which make up the channels that conduct water. Because water expands as it freezes, the formation of ice in these important tissues could lead to permanent cellular damage that would impede the plants' ability to recover from winter and resume capillary flow of water in spring.

Winterized cells enter quiescence or dormancy and require little energy for maintenance; thus, the excess amount of sugars that results from the focused productivity of summer leaves is stored safely as starch in roots. Alternatively, these sugars may be dissolved in the cytoplasm of some cells and serve as



Carbohydrates produced during photosynthesis are stored as starch during the spring and summer, powering the development of new leaves and other plant parts and, later, winter survival. During winter, these stores are tapped to maintain respiration and resist frost damage. In spring, leftover starch stores are remobilized for budburst. This carbon storage and remobilization strategy, used by deciduous trees and many perennial plants, shows a natural seasonal cycle that anticipates and responds to times of high and low resource availability and energy needs.

antifreeze, which lowers the freezing temperature and protects cells from ice formation and the associated damage.

Shutting down activity in these ways—ceasing water conductance or using dissolved sugars as antifreeze—represents extremes that serve plants well in winter: freeze avoidance or freeze tolerance, respectively. Plants such as deciduous trees may use a combination of these approaches to overwinter robustly.

Seasonal Adjustments

Like plants, humans also have seasonal shifts—whether these are based on environmental seasons or other seasons related to development, such as life stage. I suffer from seasonal allergies, so I can certainly attest to being subject to the environmentally tuned shifts that organisms undergo, such as many plants' mass release of spring pollen. Whereas some of our seasonal shifts may occur over years, rather than over the span of a calendar year, we know that seasons of maturation and growth in humans also can require periods of focused productivity supported by significant energy inputs. Certainly, parents like me who have been responsible for the energy input of rapidly growing boys will attest to this fact. Yet, despite our recognition of the environmental and developmental seasons that affect our energy requirements, the common human condition is to pursue constant action with limited attention to seasonal adjustments.

Humans, unlike plants, sometimes overlook the need for adequately anticipating when action needs to be tuned to season-like cues. The enslaved people of McLeod had no choice but to be attuned to the cycles of the seasons and the plants. Today, we have choice—but along with that liberation, we've lost a valuable connection. Accurately assessing when we are most supported—akin to the anticipation and early action of spring and high productivity of summer—is critically important. It is equally essential that we anticipate and appropriately respond to periods that require us to prepare for and engage in planned rest and pause.

"It is all too common that we humans perennially persist in a state of all-out action, as if we exist in a perpetual state of summer."

The short, overcast, and sometimes brutally cold days of winter trigger a change of pace for me, if not focus. In keeping with the style of modern society, our research continues full speed ahead because of the use of lighted growth cabinets and temperature-controlled greenhouse spaces. As much as I enjoy long walks, winter is not a time when I am drawn to linger outside. Fascinated by the leafless deciduous trees or the stalwart evergreens as they withstand the cold that I can bear only for brief moments, I often take drives and reflect on how these plants persist in winter, largely at rest. The plants' overwintering inspires me to slow down as fully as possible in the winter break between academic terms, and to rest and restore before emerging anew in the next academic season.

Although it is always critical for us to pay attention to the demands of life, even as we navigate educational or professional commitments, the recent coronavirus pandemic has amplified this need for many of us, as well as for those we mentor or lead. It was clear to me that I and members of my research team were each navigating the potential health risks differently. Additionally, the potential mental and emotional stresses of navigating a world in the midst of a pandemic had different consequences depending on whether we were near or far from family and loved ones. All these realities, which existed before and will persist after this moment, affect our abilities to be present for and engage in our research responsibilities. The importance of trying to anticipate a need for a shift in focus, equivalent to a state of rest, was high on my list as a mentor and leader. In the case of the pandemic, distinct from many other times, all but essential workers were forced into a state of pause in some regard, even as many of us attempted to keep working or learning from home.

Indeed, it is all too common that we humans simply perennially persist in a state of all-out action, as if we exist in a perpetual state of summer, with access to all the resources we may need for full productivity. The COVID-19 pandemic has been an extreme kind of forced pause, but most people have reacted by trying to work as aggressively as ever. In our quest for a “new normal,” we may not be adequately adjusting to the disruption that this crisis represents. What if we used this moment to pay more attention to the natural cycles that used to force life to slow down for part of the year, every year? When we engage in continuous action despite the fact that all cues point to a time for rest or pause, we can end up in a compromised state in which our physical, mental, or emotional capacities—the equivalent of our root-based energy stores—are depleted and we enter “enforced,” rather than carefully planned and orchestrated, pause. This forced pause can come from physical exhaustion or illnesses, chronic insomnia, or mental or emotional burnout, among other causes that prompt us to pause and rebalance physically, mentally, or emotionally.

The Gift of Plant Wisdom

During my annual spring walks to admire the brilliant red leaves that emerge post-budburst, I’m reminded to stop and reflect on how I am actively anticipating or preparing for my pending seasons—personal and professional. I’m also prompted to ask whether I’ve had an appropriate period of rest like the plants have as they emerge from winter into spring. Likewise, as I eagerly anticipate the fall colors of deciduous plants annually, I have learned to take their cue to remind myself to prepare for a “quieter” existence and to conserve energy as I may be

heading into a period of planned pause. Just as deciduous plants release leaves that would be too expensive to bear through winter, my quieter existence often consists of periods such as quarterly retreats with limited formal responsibilities, allowing me to focus on restoring and preparing for a busier period of planned commitments and responsibilities ahead.

As I write this, many people across the globe are in, or perhaps in some cases are emerging from, an enforced pause associated with the global coronavirus pandemic. Each time I am forced into pause by external factors or occurrences, I recommit to intentionally approach future pauses from a state of anticipation, focused productivity, and proactive planning, as well as preparation for rest. I’m reminded in these periods of my enslaved ancestors, and indeed all our ancestors whose lives were dictated by natural environmental seasons. This seasonally driven lifestyle included cycles of intense activity and periods of slowed pace and rest. Although we fight against it in our current lives of constant busyness, our bodies remember a need for season-driven behavioral adjustments. To thrive optimally, we need to honor these natural cycles. I’ve come to depend on plants as dedicated and persistent teachers for inspiration and guidance in these efforts. Deciduous trees bear strong witness to the wisdom of seasonal living and being, and they stand prepared to teach us these lessons every year—if only we can learn these lessons well and, better yet, aptly implement them.

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