

PERSPECTIVES



Ancient grasslands. Mosaics of forests and grasslands—as shown here for [add location of photo]—are common in the tropics and subtropics. The grasslands have long been interpreted as secondary vegetation produced by deforestation, and many are targets for “reforestation” (1). However, they have a rich endemic ancient biota adapted to frequent fires.

ECOLOGY

Ancient grasslands at risk

Highly biodiverse tropical grasslands are at risk from forest-planting efforts

By William J. Bond^{1,2}

Concerns over deforestation have led to attempts to identify suitable areas for reforestation around the world (1). The most ambitious effort to date is the World Resources Institute (WRI) Atlas of Forest and Landscape Restoration Opportunities (1). This map is linked to a global plan to reforest degraded lands to offset anthropogenic CO₂ emissions. The imme-

diate target is the reforestation of 1.5 million km² by 2020 (2, 3). Vast areas of open grassy vegetation have been identified as suitable for reforestation. But are all these grasslands secondary products of deforestations? Recent research shows that grasslands are often ancient and highly biodiverse, but it remains difficult to distinguish between primary and secondary grasslands on a large scale. Reforestation efforts thus risk converting ancient tropical grasslands to plantations.

Research on tropical grassy biomes has been remarkably neglected relative to forests (4, 5). This neglect has been attributed to the widespread perception that they are human artifacts created and maintained by human-lit fires. Yet, there is evidence for a much more ancient origin of fire-maintained grassy vegetation in regions where the climate and soils can support closed forests (see the figure). Tropical grassy biomes (grasslands and savannas) include ecosystems with a rich plant and animal life entirely restricted to open habitats (4, 6). They provide important ecosystem goods and services to the ~500 million people who live in them (5). Furthermore, the full consequences for the Earth-atmosphere system of converting grassy ecosystems to forests have not been evaluated (7). For example, changes in albedo can offset any gains in

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stored carbon as the reflective surface of grasslands, especially in the dry season, are converted to the dark absorptive surfaces of forests.

A key clue to the antiquity of grasslands is the presence of species unique (endemic) to open grassy habitats. The cerrado (savannas) of Brazil are ranked 12th on a list of global biodiversity hot spots with about 6000 plant species. Once considered poor in vertebrate species, cerrado is now proving to have a rich, endemic fauna of reptiles (8). The grassland biomes of southern Brazil and South Africa are also rich in plant species, with an estimated 3000 to 4000 in an area of 137,000 km² in southern Brazil and 3800 in 112,000 km² in South Africa (4, 9). The Atlantic coastal plain of North America is also species-rich, with some 6000 plant species (nearly a third of the North American flora), of which 29% are endemic (10, 11). Most of the endemic species occur in

the grasslands that cover most of the island were long thought to be produced by deforestation in the aftermath of human settlement a few thousand years ago (12). This narrative of deforestation as the source of grasslands was powerful enough to put off researchers from exploring the diversity of grasslands. Recent grass collections have revealed a remarkably rich grass flora, with some 40% of the 580 grass species endemic to the island. These levels of endemism are among the highest in the world for a grass flora (12). Despite clear evidence for the antiquity of Madagascar's grassland biota, it remains highly uncertain how much of the island's grasslands is a result of deforestation.

Tropical grassy ecosystems are highly flammable. They are most extensive in seasonal wet/dry climates, where high rainfall supports high productivity in the rainy season, whereas the long dry season pro-

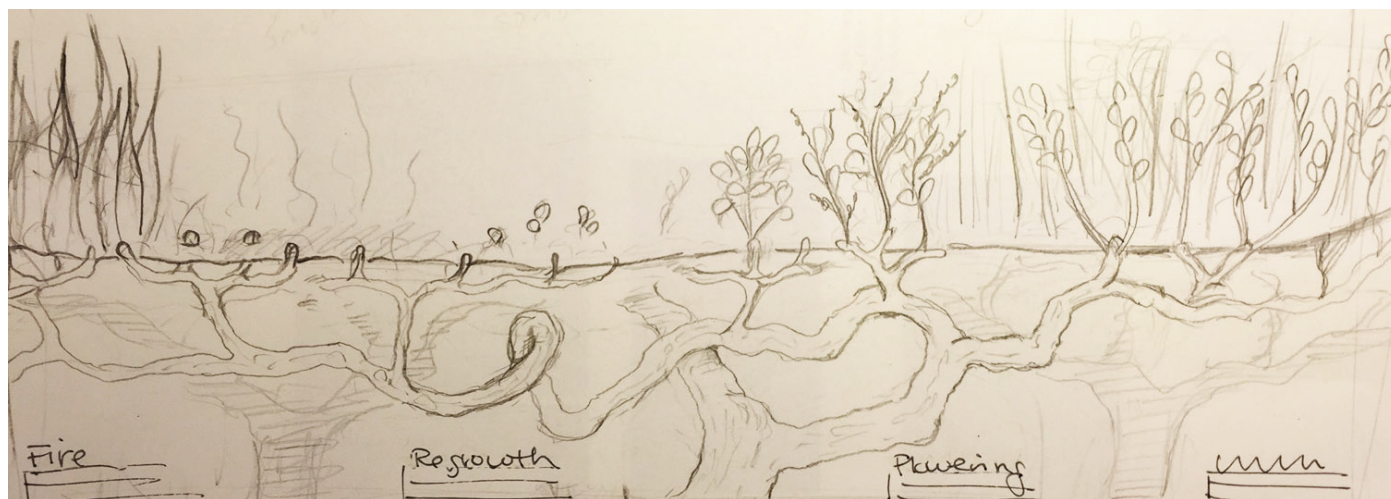
duces highly flammable grass fuels. Humid tropical grasslands burn several times in a decade; some regularly burn twice in a year. The grassy biomes of Africa alone accounted for more than 70% of the world's burnt area from 1997 to 2009.

Plants living in these highly flammable environments survive by retreating underground, developing large underground storage organs (USOs) (see the figure) that resprout rapidly after a burn (6). Nongrassy herbs (forbs) with USOs commonly flower in the first growing season after a burn before they are smothered by grass growth. Among woody plants, thick bark, insulated buds, clonal spread, and juvenile forms with USOs are adaptations to frequent grass-fueled fires (13).

"Underground trees" are a peculiar growth form characteristic of frequently

burnt savannas in South America and Africa (14). These plants have massive underground branches protected from surface fires. The leaves are borne on short stems that resprout from the buried branches after fires. Underground trees have evolved multiple times from different lineages in South America and Africa in open grassy habitats with frequent fires and, often, poor soils (13, 15).

Underground trees (geoxylic suffrutices) have close relatives that are true trees. Using a dated phylogeny, Maurin *et al.* (15) have shown that most underground trees in fire-maintained savannas in Africa originated between 6 and 2.5 million years ago, with peak divergence in the past 2 million years (15). These times of origin are remarkably similar to those obtained from phylogenetic studies of fire-adapted woody legumes in South American savannas (13). They are also consistent with fossil



Underground trees. Many tropical grassland species have large underground storage organs, resprout rapidly after fire, and have fire-stimulated flowering. Some woody species with tall tree relatives form "underground trees," with massive belowground branches supporting short aboveground stems that resprout rapidly after a fire.

pine savannas and communities embedded within them. All these systems depend on frequent fires to maintain them and are replaced by closed forests where fires are suppressed.

The Atlantic coastal plain grasslands of North America have only recently been recognised as a significant biodiversity hot spot (11). Noss attributes this oversight to misconceptions and myths, such as the myth that fires can only be ignited by humans. Similar misconceptions are widespread throughout the tropics. In Madagascar, for example, unique for its remarkable endemic forest fauna and flora,

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A distinctive feature of the flora of tropical grasslands is a marked intolerance of shade. Fire-suppression experiments have led to the elimination of long-lived forbs as a result of shading by an accumulation of dense undecomposed grass litter. Old-growth grassland plants, especially long-lived forbs with USOs, are eliminated

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by forest expansion or afforestation with pines and eucalypts. Secondary grasslands, formed after deforestation or removal of plantations, have completely different species compositions from primary grasslands (4, 6). Forbs with USOs and underground trees are particularly vulnerable, with no recovery to old-growth conditions after decades of natural succession.

These studies are revealing striking differences in old-growth versus secondary grasslands. However, the scale of analysis does not yet permit large-scale identification of old-growth grasslands. It is not yet possible to map old-growth grasslands at the scale of the WRI Atlas of Forest and Landscape Restoration Opportunities (1–3). The Food and Agriculture Organization (FAO) uses tree cover and height to classify forest and ignores the herbaceous layer (5). Yet there are profound functional differences between open woodlands with a highly flammable grassy understorey and closed forests that lack fuel to burn. Ultimately, old-growth versus secondary grasslands will have to be classified by identifying characteristics of the herbaceous layer, such as grass composition, that are visible from satellites and that are also proxies for primary grasslands.

There are many fundamental unanswered questions about grassy biomes, their function, origins, and antiquity. The recent spate of papers on these fascinating systems suggests that this neglect is coming to an end. There has been considerable progress in identifying old-growth grasslands and their ecological requirements, and this bodes well for restoring forests and the services they provide while also maintaining ancient tropical grassy ecosystems. It would be a travesty if ancient grasslands are replaced by ill-conceived forest plantation projects because of misconceptions about the origins of tropical grassy systems. ■

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GEOCHEMISTRY

Lower-mantle materials under pressure

Laboratory measurements provide a window into Earth's mantle dynamics

By Jiuhua Chen

Modern high-pressure experimental techniques have enabled us to achieve the pressure and temperature at the center of Earth (about 360 GPa and 6000 K) in laboratories. However, studies of rheological properties of minerals under controlled strain rate (creep experiments) have been limited to the pressure equivalent to that in Earth's transition zone, a depth only about one-tenth of Earth's radius. Determinations of rheological laws that govern the flows and viscosities of minerals in Earth's deep mantle have been far beyond our reach. In the absence of such critical data, the nature of mantle dynamics—such

“All the evidence lead us to a hybrid convection model—a mixture of layered and whole-mantle circulations”

as whether the convection involves the entire lower mantle, yielding a chemically homogeneous deep mantle—remains controversial. Discovery of the breakdown of ringwoodite into the denser bridgmanite and magnesiowüstite phases at 24 GPa (1) removed the need for a major chemical discontinuity in Earth inferred from observations of a strong seismic reflector at 660 km depth. On page XXX of this issue, Girard *et al.* (2) report on the detailed rheological nature of this bridgmanite plus magnesiowüstite mineral aggregate, shedding more light on the mantle convection. The integration of brilliant synchrotron radiations and rotating apposed anvils enables creep experiment for large strain at pressures equivalent to that in Earth's lower mantle.

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Nearly 90% of the lower mantle is occupied by the minerals bridgmanite and magnesiowüstite. Bridgmanite is believed to be the rheologically strongest phase at high pressure and high temperature among all dominant minerals in the shallower mantle (3), giving rise to a high viscosity of the lower mantle relative to the upper mantle and the transition zone. In their creep experiment on these two minerals directly converted from natural olivine, Girard *et al.* not only recognized that bridgmanite is substantially stronger than magnesiowüstite and that a large fraction of the strain is accommodated by magnesiowüstite, but also observed a tendency of strain weakening of bridgmanite when large strain (>40%) is applied. These observations may indicate shear localizations in the lower mantle—a result that would have an impact on the mantle dynamics.

If we assume that large enough strains occurring in deep mantle convection eventually produce interlinking of the weak magnesiowüstite phase in the microstructure of the mineral aggregate due to the shear localization, then a transition of its rheological behavior from a load-bearing framework (LBF) phase to an interconnected weak layers (IWL) phase might be expected on the basis of the semitheoretical model described by Handy (4). Taking 2×10^{21} Pa·s and 1×10^{19} Pa·s as the viscosities of bridgmanite and magnesiowüstite, respectively, at the top of the lower mantle (5), the viscosities of the mineral aggregate for the IWL and LBF regions would be 4.5×10^{19} Pa·s and 1.5×10^{21} Pa·s, respectively (assuming a bridgmanite/magnesiowüstite volume ratio of 7:2). This contrast in viscosity, as a result of shear localization, provides us with key information into the lower mantle such as long-lived geochemical reservoirs and the absence of seismic anisotropy in the majority of the lower mantle. The result may actually have much broader implications for our understanding of the lower mantle.

High viscosity of the lower mantle is considered to be the major resistance slowing down the sinking rate of a subducting slab (6). This is true at the early stage of convec-