

# Uncertain sinks in the shrubs

Christine L. Goodale and Eric A. Davidson

Replacement of grassland by shrubland, which is occurring on a large scale in the United States, is thought to lock up considerable amounts of carbon. This 'carbon sink' may be much smaller than previously estimated.

Balancing the global carbon budget just got more difficult. For decades, there has been debate over what happens to the carbon dioxide released from the burning of fossil fuels and clearing of tropical rainforests. About half of it accumulates in the atmosphere<sup>1,2</sup>, prompting concerns about global warming. The ocean and land take up the rest, acting as carbon sinks, and understanding where and why these sinks occur is essential for managing them in the future. Now, new field measurements cast doubt on the estimated size of one potentially large but poorly quantified carbon sink — that of woody shrubs when they encroach into and replace grassland, a process that has been thought to lock up large amounts of extra carbon. As they describe on page 623 of this issue, Jackson *et al.*<sup>3</sup> show that there are smaller increases in carbon storage than anticipated, and in some cases actual reductions.

There is general agreement that land in the Northern Hemisphere acts as an important carbon sink. Yet estimates of its exact size, and the specific locations and

contributing factors, vary greatly, due in part to different measurement approaches. Calculations based on measurements of carbon dioxide and oxygen in the atmosphere<sup>1,2</sup> nearly always produce larger estimated sinks for North America and Eurasia ( $0.6\text{--}2.7 \times 10^{15}$  grams — petagrams — of carbon per year) than do those based on ground measurements of forest growth ( $0.6\text{--}0.7 \text{ Pg C yr}^{-1}$ ).

Last year, however, a carbon budget produced for the continental United States partly reconciled top-down (atmospheric) and bottom-up (land-based) methods by including estimates of both forest and non-forest sinks<sup>4</sup>. Together, the bottom-up estimates ( $0.4\text{--}0.7 \text{ Pg C yr}^{-1}$ ) roughly matched those from the top-down approach ( $0.7 \pm 0.5 \text{ Pg C yr}^{-1}$ ). This reconciliation depended on the existence of a rather large sink (about  $0.13 \text{ Pg C yr}^{-1}$ ) in the rangelands of the western United States<sup>4,5</sup>. The suppression of fires and overgrazing have favoured the expansion of trees and woody shrubs into grasslands<sup>6</sup>, over an estimated area of as much as 220 million hectares in the United States<sup>4,5</sup>. This 'woody encroachment' formed 18–34% of the total estimated sink for carbon in the continental United States — it was by far the largest non-forest sink, and the least secure term in the land-based carbon budget<sup>4</sup>. Jackson and colleagues' measurements<sup>3</sup> add further uncertainty to these estimates.

The authors studied six pairs of grassland and woody-shrubland sites (Fig. 1) along a rainfall gradient in the southwestern United States. They found that conversion of grassland into shrubland increased the amount of carbon in vegetation, but usually only by a small amount. Stocks of organic carbon in soil also increased slightly in the dry sites. In the wetter sites, however, carbon stocks decreased, particularly in the top metre of soil. On net balance, the drier sites gained a small amount of carbon and two of the three wetter sites lost it. These results are consistent with a literature review showing that soil carbon decreases when pastures are planted with trees, with larger decreases occurring at wetter sites<sup>7</sup>. If the sinks investigated by Jackson *et al.*<sup>3</sup> are typical of other sites, these results indicate that the sink in the United States caused by woody encroachment<sup>4,5</sup> was substantially overestimated (Fig. 2).

Why did soil carbon decrease at the wet-

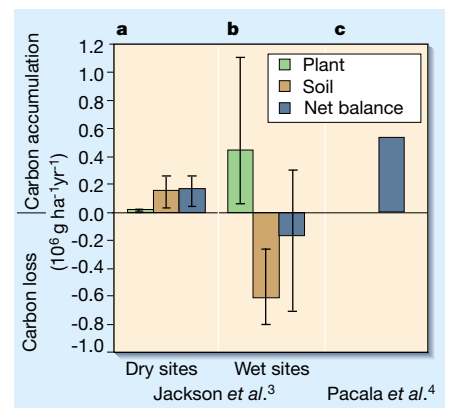


Figure 2 Carbon accumulation and loss due to expansion of shrublands into grasslands. a, Jackson *et al.*<sup>3</sup> report low rates of carbon accumulation in shrubland plants and soils at dry sites in the southwestern United States. b, The authors<sup>3</sup> found that plant carbon increased at wetter shrubland sites in the same region, but so much carbon was lost from the soil that there was a net loss to the atmosphere. Means and ranges are shown for three dry sites and three wet sites. All of these sites had lower rates of carbon accumulation than the presumed mean, depicted in c, for all US non-forest, non-cropland areas reported by Pacala *et al.*<sup>4</sup>. If this higher mean sink due to woody encroachment in the western United States were correct, the US carbon sinks calculated by atmospheric models and by ground-based measurements would appear to be nearly reconciled. The results of Jackson *et al.* cast doubt on that conclusion.

ter sites? In soil, organic-carbon stocks represent the net balance between plant inputs of carbon and subsequent losses through erosion, leaching, and decomposition by microbes. For soil carbon to decrease, either inputs decreased or losses increased (or both). Grasses usually allocate more of their production to roots than to shoots<sup>8</sup>, and most of the roots are in the top metre of soil. Furthermore, grassland productivity correlates strongly with rainfall<sup>8</sup>, so that grassland soils in the wet end of the gradient receive more root input of carbon.

When shrubs invade grasslands, carbon input to the topsoil may decrease because the woody species allocate less of their total production below ground, and what they do send to roots is distributed more deeply<sup>9</sup>. Because much of the carbon in soil decomposes slowly, several decades must pass after



Figure 1 On site — a view of the Sevilleta area, one of the sites where Jackson *et al.*<sup>3</sup> conduct their long-term research.

vegetation changes before a new equilibrium is approached, and so Jackson *et al.*<sup>3</sup> chose shrublands that were at least 30 years old. The lower soil-carbon stocks in shrublands that they measured at the wet end of the rainfall gradient indicate that inputs from woody invaders during the past 30–100 years were less than losses of old soil carbon from the grasses that previously occupied the site. This process is presumably continuing on lands where woody encroachment is more recent.

On the dry end of the gradient, Jackson *et al.* found little change in soil carbon following woody encroachment, suggesting that there was little change in production below ground. This explanation is speculative, as Jackson *et al.* did not directly measure inputs and losses of soil carbon, a very difficult task. Unfortunately, the authors also did not measure carbon stocks in woody roots (those of 1 cm or more in diameter), and so the sink in deeply rooted woody shrubs is probably an underestimate.

Woodlands, savannas, shrublands and grasslands cover about 40% of the Earth's surface<sup>10</sup>, and so their potential role as carbon sinks — or sources — is a key factor in the global carbon budget. Measuring the effects of woody encroachment at particular sites is one challenge; extrapolating the results to regional or larger scales is quite another. Particular sites are certainly large sinks for carbon<sup>11</sup>, but the global extent of grassland replacement by shrubland is highly uncertain<sup>3,4</sup>. For a few regions, analyses of historical aerial photographs or satellite data have produced estimates for the extent of encroachment (ref. 12; G. P. Asner, personal communication). Yet the results of Jackson *et al.*<sup>3</sup> complicate these assessments by showing that increases in plant biomass above ground may be more than offset by losses of carbon from soil. This cancelling of gains in carbon above ground with losses below ground has already been demonstrated for individual sites<sup>13</sup>, but we now have evidence of a regional phenomenon that appears to vary somewhat predictably along a climatic gradient.

What are needed are more reliable regional estimates. That will require comprehensive assessments of the extent to which shrubs are replacing grassland, along with field measurements and model simulations of the size and variability of plant and soil carbon stocks across a range of climate conditions.

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HIV

## A tough viral nut to crack

Roger J. Pomerantz

HIV cannot multiply in certain human cells unless it expresses a protein called Vif, the function of which has finally been revealed. It seems that it overcomes a human protein that would otherwise block viral replication.

Nowadays, researchers generally succeed in working out what viral proteins do within a few years of their discovery. This is certainly the case for nearly all proteins from the type 1 human immunodeficiency virus (HIV-1), whose genome is arguably the most extensively studied 9,700 or so bases of genetic sequence on the planet. Nonetheless, one of the HIV-1 proteins has remained an enigma wrapped in a riddle since its discovery in the mid-1980s (refs 1, 2). From the report by Sheehy and colleagues<sup>3</sup> on page 646 of this issue, it seems that the mystery has been solved, at least in part.

The protein in question is called Vif, for 'viral infectivity factor': it is an accessory protein in HIV-1 that is also found in all other primate immunodeficiency viruses. Viral accessory proteins are generally not needed for replication and survival; they are neither structural nor regulatory. But they are needed under certain 'stressful' condi-

tions imposed on the virus by its cellular home. Vif seems to be largely unique among HIV-1's accessory proteins. For example, if certain human immune cells — T lymphocytes, monocytes or macrophages, the main reservoirs for HIV-1 *in vivo* — are infected *in vitro* with HIV-1 strains carrying mutant Vif, those strains produce progeny that are, to all intents and purposes, 'dead'<sup>4</sup>. By contrast, mutation of other HIV-1 accessory proteins, such as Nef, Vpr and Vpu, leads to debilitated but still reproducing viruses.

It turns out that HIV-1 with a mutant Vif protein can produce infectious virions — viral particles — from only a few select human cell lines ('producer' cell lines)<sup>5</sup>. When infected with Vif-deficient viruses, certain producer cells, described as 'non-permissive', yield defective progeny viruses that cannot infect target cells and in which reverse transcriptase, a crucial viral enzyme, is largely inactive<sup>4,6,7</sup>. But infectious, replicating virions can be produced in the absence of

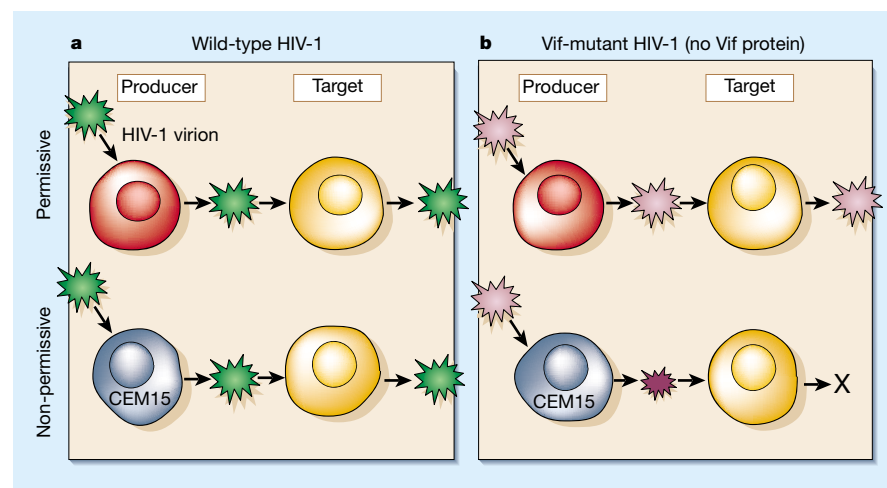


Figure 1 How HIV-1 can overcome our cells' defences. The crucial HIV-1 protein here is Vif. a, Normal, infectious HIV-1 can be produced in most human cell types ('producer' cell lines) and can infect and reproduce in most target cells. b, HIV-1 particles that lack Vif can produce infectious progeny only in 'permissive' cell types. Non-permissive cells produce non-infectious progeny. Sheehy *et al.*<sup>3</sup> have found that non-permissive cell types express the protein CEM15, which therefore presumably blocks the production of new, infectious viral particles from Vif-deficient HIV-1. By extension, the Vif protein must be required to overcome CEM15, explaining why normal HIV-1 can produce infectious viral particles in non-permissive cells (a). How Vif suppresses CEM15 is not known.