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Pasture soils as carbon sink

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average, male success when discussing how males should distribute themselves between leks of different sizes. We illustrated the effect of lek size on proportion of copulations accruing to males by calculating a composite skew index for each lek, rather than showing the relationships for each rank of male. This point remains unaffected by the criticism by Mackenzie *et al.* The model as well as all analyses of the empirical data deal solely with proportions of copulations accruing to males of different rank, however. What requires a biological explanation is not the drop in skew, but the fact that males of the same rank get different proportions of the copulations on a lek depending on the lek size.

Mackenzie *et al.* use empirical data to suggest that the conclusions of our paper are unlikely to be general. They justify this by showing that the variation in male mating success not explained by random mating does not covary with lek size in an interspecific comparison. We do not think that this is an adequate test of our model, as the ability of top males to monopolize matings is likely to vary across species. Consequently, the interaction between lek

size and the proportion of copulations accruing to a male of a given rank will vary between species. Also, the variance in mating success generated by random events is likely to differ between species<sup>5</sup>. Hence, we would not expect to find a cross-species correlation between lek size and deviation from a Poisson distribution of copulations. The intraspecific tests described by Mackenzie *et al.* are more interesting, but at this stage are too preliminary to allow evaluation.

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## Pasture soils as carbon sink

SIR — Fisher *et al.*<sup>1</sup> draw much-needed attention to the important role of deep tropical soils and tropical land use in the global carbon cycle. They show that African forage grasses planted in South American cattle pastures have prolific root systems extending below the plough layer. They calculate that the enhanced soil carbon storage resulting from increased root inputs may be large enough to be the 'missing sink' needed to balance the global carbon budget<sup>2</sup>. Hence, the conversion of savannas to cattle pastures is presented as a win-win situation, because excellent sources of forage for cattle also purportedly reduce accumulation of heat-trapping CO<sub>2</sub> in the atmosphere. We believe that Fisher *et al.* have overestimated the potential for pasture soils to be a significant carbon sink, and we also point out the deleterious effects of introduced African grasses owing to their

tendency to invade native savanna vegetation and their high flammability.

First, the results of Fisher *et al.* pertain only to savanna areas that lack significant woody vegetation; this excludes most of the Brazilian cerrado and the Amazonian rainforests, which are also being cleared and converted to cattle pastures with exotic grasses. These ecosystems lose carbon on conversion because of the loss of significant above-ground biomass.

Second, Fisher *et al.* have assumed that their measured increases in soil carbon during the 3–9 years after pasture creation would continue indefinitely. This extrapolation is incorrect, because rates of soil microbial respiration will also increase as organic matter accumulates. Because the higher carbon inputs from pasture grasses are matched by increased microbial decomposition, the soil will eventually approach a new steady-state carbon inven-

tory. The rate of net carbon accumulation is greatest for the first few years after an increase in carbon input, but approaches zero at steady state. The time required to establish steady state (or near steady state) depends on the decomposition rate of soil organic matter. Using <sup>14</sup>C from the fallout of nuclear weapons testing as a tracer, it has been shown that most of the carbon in the top metre of tropical soils has a mean residence time of up to a decade<sup>3,4</sup>. Under these conditions, the annual rate of net carbon accumulation after 20 years will drop to about 10% of the net carbon accumulation observed during the first three years following pasture establishment. A sustained carbon sink of the magnitude suggested by Fisher *et al.* would require continued establishment of new pasture, as the net carbon sink associated with older pastures declines.

Third, bad management and poor productivity of African grasses are common in much of South America. The studies by Fisher *et al.* come from experimental stations where production is presumably optimized. Many (and perhaps most) pastures planted with *Brachiaria* in both forested<sup>5</sup> and savanna<sup>6</sup> regions of Brazil are in some stage of degradation, usually due to overgrazing, extensive use of fire, invasion by unpalatable species and soil compaction. Degraded pastures typically have little grass cover and low inputs of carbon to the soil<sup>7</sup>. Unfortunately, too few data exist to estimate quantitatively how much pasture land is being managed well. To extrapolate a carbon sink across 35 million hectares of South American pastures, however, Fisher *et al.* need to provide some evidence that good pasture management is common over that large area. In contrast, several lines of evidence indicate that less than optimal grass yield is common, including reports of loss of nutritional value of African grasses during the dry season<sup>8</sup>, failure to maintain a legume association<sup>6,9</sup> and infestations of spittlebug<sup>10</sup>.

Finally, increased use of African grasses will result in further biotic impoverishment of ecosystems. Multi-species communities are being replaced by monocultures of exotic grasses. The remaining native savannas are also threatened by invasion of exotic species well adapted to displacing native grasses, through their rapid growth rate, high seed production, fast germination and colonizing ability<sup>11–13</sup>. In addition to the increased probability of intentional fires escaping from managed pastures, the exotic species that invade nearby, native savanna are highly flammable and burn at a higher temperature than native grasses<sup>13</sup>, potentially altering the frequency, intensity and extent of fire. We can thus expect functional as well as compositional change to these ecosystems.

We acknowledge that exotic grasses may offer promise by increasing productivity in

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many tropical pastures. If productivity can be sustained, the high economic reward per unit area of well-managed pastures might reduce demand for large-scale clearings of forests and savannas to meet local agricultural and economic needs. A globally significant carbon sink is, however, unlikely to be a virtue of this land use and cannot be used to justify it. Moreover, the effect of invading exotic species on native vegetation must also be considered before singing the praises of this new trend.

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FISHER *ET AL.* REPLY — The comments by Davidson *et al.* about the rainforests and the wooded communities of the cerrados are not relevant to our paper<sup>1</sup>, which was about the 35 million hectares (MHa) of treeless grasslands in Colombia and Venezuela and the 50 MHa (24%) of the cerrados of central Brazil that have no significant woody component (*Campo limpo* and *Campo sujo*<sup>14</sup>). It is on the latter, which have less fertile soils, that most of the 35 MHa of introduced pastures<sup>15</sup> have been sown in the past 30 years. The plant communities of the cerrados with a significant tree component are on more fertile soils, and when cleared have normally given way to cropping, largely because the economics of cattle production will not support the high cost of mechanical clearing.

We did not forecast that the rates of C sequestration will continue indefinitely. We measured rates of C sequestration of 2.9–14.7 t Ha<sup>-1</sup> yr<sup>-1</sup> in the soil under pastures of introduced grasses compared with the native savanna on a farmer's fields and at Carimagua research station in the eastern plains of Colombia. We hypothesized that if this process is general in sown pastures in the neotropical savannas, then the amount of C sequestered could be large enough to be important.

We do not yet know the dynamics of C in the soil under our pastures. In the same samples from Carimagua that we reported in our paper, not only are the C:N ratios of the soil under savanna unusually high at 21.5, but also we measured a shift to 33.2 after nine years of introduced grass pasture, five of them with a legume (s.e. of difference ±6.57,  $n=7$ ,  $P<0.001$ ). For this to occur, the C:N ratio of the newly accumulated soil organic matter must be very high. We do know that the C:N ratios of litter of the African grasses are unusually

high. For above-ground litter of *Brachiaria decumbens*, *B. dictyoneura* and *B. humidicola* and *Andropogon gayanus* they are 74.8–193.5 (ref. 16), and for fine and coarse roots of *B. dictyoneura* and *B. humidicola* they are 158 and 224 (ref. 17). It would be dangerous to apply conventional wisdom to organic matter derived from this litter because it is likely to be less easily broken down by soil biota, and therefore the soil C may have longer residence times. We accept that there will be a new equilibrium, but at what level and when is an open question.

With regard to management, we have measured C sequestration of 2.9 t Ha<sup>-1</sup> yr<sup>-1</sup> in a 17-yr-old pasture of *A. gayanus* that had been subjected to mismanagement by burning, over- and undergrazing at least as bad as the worst farmers' fields. This rate is the same as in pure grass pastures reported in our paper, whereas our data also show that well-managed pastures with a good legume balance can sequester C at up to five times this rate.

All grasses lose some nutritional value during the dry season, but the introduced ones at all times have higher quality than the savanna species they replace<sup>18</sup>. This, and their deep-rootedness, which allows them to grow longer into the dry season, are the main reasons farmers have sown 35 MHa in the Brazilian savannas<sup>19</sup>. There have been some problems with persistence of tropical legumes sown with introduced grasses, in part due to their different photosynthetic pathways<sup>20</sup>. But *Arachis pintoi*, the legume in one of our experiments, has persisted in mixture with contrasting grasses in the Colombian Llanos under differing managements for as long as 13 years<sup>21</sup>. The Brazilian experience is shorter, but there are no recorded failures once the legume is well established. Spittlebug has been a problem in some *Brachiaria* spp. in some humid areas of the neotropical savannas.

## Conserved cell and organelle division

STR — The process of organelle division in eukaryotes is poorly understood and no genes involved in this process have yet been isolated. In prokaryotes, from which both chloroplasts and mitochondria probably evolved<sup>1</sup>, several genes essential for cell division have been identified. The best characterized encodes the protein FtsZ, which forms a ring at the leading edge of the cell division site<sup>2</sup>. It has been proposed that FtsZ is a prokaryotic cytoskeletal element and possibly an evolutionary progenitor of tubulin<sup>3</sup>. The role of FtsZ in prokaryotic cell division suggested to us that a similar protein might be involved in the division of eukaryotic organelles.

We used the amino-acid sequence of *Escherichia coli* FtsZ as a probe in a homology search of the Expressed

Breeding for resistance to it in *Brachiaria* spp. is a major objective of plant improvement both at CIAT and by the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) in Brazil<sup>22</sup>.

We share the concern about the conservation issues raised by Davidson *et al.*, but to address them was outside the scope of our paper. *Panicum maximum*, *Hyparrhenia rufa* and *Melinis minutiflora*, African grasses introduced to the neotropics almost 100 years ago, do invade native savanna<sup>11</sup>, particularly in the absence of fire. We have looked for, but not found, invasion of undisturbed savanna by *A. gayanus* or *Brachiaria* spp., the species in our experiments and the main ones sown over the past 20 years in the neotropics.

A large portion of the neotropical savannas has been replaced by sown pastures and crops for economic and other reasons. Our point is not that savannas and grasslands ought to be replaced by introduced pastures, but that, when they are, the pastures can have beneficial effects in terms of C sequestration in the soil.

We agree with Nepstad *et al.*<sup>7</sup> that there is a need to understand the dynamics of soil-plant processes associated with C sequestration in tropical American soils. We would extend this to include the introduction, degradation and reclamation of pastures based on African grasses in tropical America and the trade-offs involved.

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Sequence Tag database dbEST<sup>4</sup>. Complementary DNA from *Arabidopsis thaliana*, with no assigned matches in the database but exhibiting a small stretch of homology to *E. coli* FtsZ, was identified, obtained from the Arabidopsis Biological Resource Center, and sequenced fully. The open reading frame encoded a protein of 433 amino acids ( $M_r$  45,600) with significant homology to FtsZ sequences from several prokaryotes (Fig. 1). Noteworthy in the *Arabidopsis* sequence are conservation of the glycine-rich 'tubulin signature' motif which is common to both FtsZs and tubulins and is important for GTP binding<sup>5</sup>. All but one of the residues identical in bacterial FtsZs and tubulins<sup>6</sup> are also conserved.

The *Arabidopsis ftsZ* gene seems to be most closely related to the prokaryotic