Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the "Birch effect"[†]

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Summary Observations on the net carbon exchange of forests in the European Mediterranean region, measured recently by the eddy covariance method, have revived interest in a phenomenon first characterized on agricultural and forest soils in East Africa in the 1950s and 1960s by H. F. Birch and now often referred to as the "Birch effect." When soils become dry during summer because of lack of rain, as is common in regions with Mediterranean climate, or are dried in the laboratory in controlled conditions, and are then rewetted by precipitation or irrigation, there is a burst of decomposition, mineralization and release of inorganic nitrogen and CO_2. In forests in Mediterranean climates in southern Europe, this effect has been observed with eddy covariance techniques and soil respiration chambers at the stand and small plot scales, respectively. Following the early work of Birch, laboratory incubations of soils at controlled temperatures and water contents have been used to characterize CO_2 release following the rewetting of dry soils. A simple empirical model based on laboratory incubations demonstrates that the amount of carbon mineralized over one year can be predicted from soil temperature and precipitation regime, provided that carbon lost as CO_2 is taken into account. We show that the amount of carbon returned to the atmosphere following soil rewetting can reduce significantly the annual net carbon gain by Mediterranean forests.

Keywords: carbon balance, carbon mineralization rates, Mediterranean climate, Mediterranean forest, rain pulse, soil rewetting, soil temperature, soil water, summer rainfall events.

Introduction

This synthesis paper is concerned with the loss of carbon from Mediterranean- and savannah-climate ecosystems following soil rewetting by rainfall after a period of drought. One aim is to acknowledge H.F. Birch's path-breaking contributions made some 45 years ago, and thus to explain the origins of the "Birch effect" appellation and to justify its use today. A further aim is to outline current explanations for the Birch effect, because understanding the processes involved is a developing area of research. A third aim is to demonstrate by observation and experiment that the Birch effect, originally elaborated in terms of nitrogen release from soil samples in the laboratory, occurs at large spatial scales as manifest by CO_2 emissions, and consequently needs to be taken into account in regional-scale carbon budgets.

About 47% of the surface of the Earth can be classified as drylands (UNEP 1992). Most arid lands occur between latitudes 20 and 35° and are characterized by low precipitation, high temperatures and high potential evaporation. Semi-arid lands occur to the north and south of the arid zones and include Mediterranean, savannah and monsoonal climates.

The warm temperate climate of lands around the Mediterranean is characterized by dry summers and wet, sometimes stormy, winters, originating from the anti-cyclones of the desert zone in summer, and from travelling cyclonic disturbances of middle latitudes in winter. This regional climate has given its name to climatically similar areas around the world, particularly in Africa, South America, South Australia and Western Australia, that occur largely between latitudes 30 to 40° both north and south of the equator. The vegetation of such

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areas, with various regional names including garrigue, maquis, macchia, chaparral, mattoral, fynbos and mallee, commonly comprises shrubs and small trees, frequently evergreen with tough or drought-deciduous leaves, and annual herbs and grasses. The total global area of lands with a Mediterranean-type climate is about 2.75 million km² (Rambal 2001).

H.F. Birch did pioneering experiments (Appendix 1) in the 1950s and 1960s while working at Muguga, near Nairobi, a region with a savannah climate. In this region, large scale pressure systems of the Indian Ocean give rise to a short summer rainy season from late March to May, when winds are from the northeast, and a dry winter season of stable weather with little rainfall from June to August, when winds are from the southeast. The climate at Muguga is moderated by altitude, is cool and has a rainfall of about 1100 mm, whereas rainfall on the drier lands to the east may be less than half that.

Regions with savannah climate extend poleward from near the equator to between latitudes 25 and 30° and cover large areas in Central and South America, especially Mexico and Brazil, eastern India, southeast Asia, central, eastern and western Africa and east and northern Australia, with regional names that include miombo and cerrado. The best current estimate of the global area of tropical savannahs and grasslands is 27.6 million km², to which may be added 5 million km² of temperate savannahs (House and Hall 2001).

A common feature of Mediterranean- and savannah-climate ecosystems is a period of sustained drought during which soils dry and are substantially rewetted only by sustained rainfall at the end of the drought season. The response of soil processes consequent on rewetting is likely to be common to a range of vegetation types in both climate systems. These biomes are representative of the more widely distributed semi-arid areas throughout the world.

The global pool of carbon in soils exceeds that in vegetation by about 4:1. The regional mean carbon stock in soils and vegetation ranges from a ratio of about 1:1 in tropical forests to 5:1 in boreal forest to 17:1 in deserts and wetlands, with residence times ranging from 10 years in tropical savannahs to more than 200 years in deserts and tundra. Thus, changes in soil carbon stocks are at least as important as changes in vegetation carbon stocks to the global ecosystem carbon budget, and gains and losses of soil carbon are particularly important to the atmospheric carbon budget and to global warming (Dixon et al. 1994, Schlesinger 1997). Although rates of carbon accumulation may be low in arid and semi-arid climates, the residence time of soil carbon is long so that appreciable amounts of carbon are stored in these soils.

The work of H.F. Birch

Birch began his research career at the Imperial College of Tropical Agriculture, Trinidad, and, following a period in Jamaica, was moved by the U.K. Colonial Office to Tanganyika in 1945 to work on extraction of the anti-malarial alkaloid, quinine, from the bark of trees of *Cinchona* spp. This work was terminated some five years later when mass production of syn-

thesized anti-malarial drugs, developed during World War II, became available. Birch then moved at the behest of the Colonial Office to the East African Agricultural and Forestry Organization (EAAFRO), at Muguga, near Nairobi, Kenya, as Head of the Agricultural Chemistry and Soils Department (Appendix 1).

While at the EAAFRO, Birch did innovative experiments in which he showed that cycles of drying and wetting of soils stimulate mineralization of soil organic matter, leading to release of mineral nitrogen and loss of soil carbon.

Over the next 10 years, through laboratory experiments and observations in agricultural fields, Birch meticulously characterized the impacts of soil drying and wetting cycles on nitrification, release of mineral nitrogen and loss of carbon in a series of papers, most of which were published in *Plant and Soil* (1958, 1959, 1960, 1964) (Appendix 1). In the course of the work he demonstrated and characterized the following phenomena associated with soil wetting and drying cycles: (1) a high rate of humus decomposition and rapid mineralization follows rewetting of dry soils; (2) in continuously moist conditions, there is a release of nitrogen, much of it as NO_3, and phosphorus that is usually re-fixed, and a loss of soil organic carbon as CO_2; (3) enhanced decomposition and mineralization declines with time after rewetting; (4) the amount of carbon mineralized, and thus of CO_2 emitted, and the magnitude of the nutrient pulse in each cycle depends on the amount of carbon present, with the result that mineralization falls off in successive cycles as the amount of carbon declines; (5) the more severe the drying (i.e., the longer the period or the higher the drying temperature), the larger the amount of decomposition and mineralization on subsequent wetting; (6) intermittent drying increases overall mineralization with a cumulative effect on nitrogen release and carbon loss; (7) rapid large increases in populations of soil bacteria are concurrent with these changes on rewetting; and (8) more nitrogen and carbon are released by soils subject to wetting and drying cycles than by continuously moist soils.

These phenomena have become known collectively as the Birch effect. Although Birch was the first to provide a detailed characterization of the processes involved, he was not the first to notice them. Thus, in 1987, B.N. Richards wrote "the stimulating effect of alternating dry and moist phases on mineral nitrogen production was first recorded by A. N. Lebedjantzev in 1924. Both physicochemical (Paul and Tu 1965, van Schreven 1964) and biological (Birch 1964) interpretations have been proposed to account for this phenomenon." Today, four main hypotheses have been proposed to explain the nutrient pulse and, by implication, the CO_2 pulse: (1) drying and rewetting shatters soil aggregates and exposes previously unavailable organic substrates for decomposition (e.g., Denef et al. 2001); (2) microorganisms killed by soil drying are decomposed on rewetting to release their nutrients (e.g., Bottner 1985); (3) there is a spontaneous rapid increase in microbial biomass and fungal hyphae in response to the availability of water (Griffiths and Birch 1961, Jager and Bruins 1974, Orchard and Cook 1983, Scheu and Parkinson 1994); and (4) there is a microbial hypo-osmotic stress response (Kieft et al. 1987, Fierer and

Schimel 2002, 2003). This last, comparatively new, hypothesis is elaborated later.

These hypotheses are not mutually exclusive, and they are unlikely to have identical implications for soil carbon dynamics. For example, as pointed out by a helpful reviewer, different carbon sources would contribute to the pulse depending on whether emissions of CO_2 were caused by the breakdown of soil aggregates, enhancement of microbial populations or turnover of osmo-regulants. With increasing interest in the Birch effect, because of its impact on CO_2 emission budgets in regions with savannah and Mediterranean climates, we may anticipate further critical experimentation to test these hypotheses. Birch was convinced that the cause of enhanced mineralization on the wetting of previously dry soil is a rapid, immediate explosion in microbial populations, particularly in the organic surface soil layers (Griffiths and Birch 1961), and this has subsequently been demonstrated in several studies (e.g., Orchard and Cook 1983, Orchard et al. 1987), but not in all.

Birch's primary interest was not in the carbon budget of soils, or the concentration of CO_2 in the atmosphere, but in the mineralization of nitrogen and its availability for crop growth. He demonstrated that enhanced nitrification resulted from soil rewetting after drought in the field or drying in the laboratory, and in field trials he showed that this increased growth of several tropical crops. Birch's observations have been confirmed by experimental rewatering of crops with simulated rainfall in Uganda and Senegal (Dick et al. 2001, 2005). These authors found that the initial response after a simulated small rainfall event (10 mm) led to nitrification, but a larger rainfall event (25 mm) that wetted the soil more thoroughly led to denitrification. Like Birch, Dick et al. (2001, 2005) demonstrated that the N mobilized in the soil had a fertilizing effect of economic significance, especially for subsistence farmers unable to afford nitrogen fertilizer. They also found, perhaps unsurprisingly, that the magnitude of these soil responses to rewetting was far larger in agro-forestry systems where the tree component was the nitrogen-fixer *Calliandra calothyrsus* Meissn., adding nitrogen-rich debris of leaves and roots to enrich the soil organic matter, than in agro-forestry systems where the tree component was the non-nitrogen fixer *Grevilla robusta* A. Cunn. ex R. Br.

Additionally, Dick et al. (2001, 2005) have added a new dimension to the Birch effect of potential significance to climate change. Concurrent with the enhanced decomposition and mobilization of mineral nitrogen and pulses of CO_2 emissions, they identified pulses of N_2O emissions associated with nitrification and denitrification. Soils under *C. calothyrsus* emitted 75 times more N_2O than soils under *G. robusta* after a heavy rainfall event, but emissions were similar after a light rainfall event.

Although much of the work of Birch and his successors has focussed on the microbiological processes and chemical transformations that can be elucidated with samples in the laboratory and on agricultural plots, the Birch effect can also be observed in response to rainfall, and induced by irrigation, at a wide range of spatial scales in the field. In the following sections, we present examples and analyses of the enhanced emissions of CO_2 resulting from the Birch effect over spatial scales ranging from a few cm^3 in laboratory incubations to areas of $1 km^2$ or more in the field.

Field observations: stand scale

Eddy-flux observations of net ecosystem CO_2 exchange

In the first instance we focus on field observations at the $1 km^2$ scale and their significance for sequestration of atmospheric CO_2. Through technical development in the mid-1990s, it became possible to measure the net ecosystem exchanges (NEE) of CO_2 between vegetation and the atmosphere almost continuously, with half-hourly resolution, by the technique of eddy-covariance (Moncrieff et al. 1997, 2000). Today, annual carbon budgets for an area of vegetation over a period of five or more years are not uncommon (e.g., Valentini 2003). During the latter part of the 1990s, the European Commission funded such measurements on several temperate forest sites in Europe through the EUROFLUX project (e.g., Valentini et al. 1999, Janssens et al. 2001, Valentini 2003). Toward the end of the 1990s, a parallel project, known as MEDEFLU, was initiated for macchia and forest sites with Mediterranean climate in southern Europe (Miglietta and Peressoti 1999). Whereas the EUROFLUX forest sites in temperate northern Europe, or in the mountains further south, rarely experience long dry periods, summer droughts are characteristic of the MEDEFLU sites around the Mediterranean Sea in southern Europe. Continuous measurements of the NEE of CO_2 were made at these sites over extended periods (Aubinet et al. 2003). In Figures 1–3, we show examples of the impact of intermittent rainfall on NEE of CO_2 from two forest sites and a third site comprising abandoned agricultural fields and macchia. Site details for the two forest sites are given in Table 1.

Figure 1 shows the annual pattern of CO_2 uptake at the Mitra site in Portugal of cork oak (*Quercus suber* L.) and holm oak (*Quercus ilex* L. ssp. *rotundifolia*). During the spring and early summer, when rainfall events were frequent, there was a well-developed uptake of CO_2. As summer developed and rainfall became less frequent and eventually ceased, CO_2 uptake fell to near zero. When rainfall resumed, even small amounts resulted in large emissions of CO_2 that declined over several days. Two further rather larger rain events led to a repetition of large emissions followed by progressive decline until the soil became sufficiently wet for CO_2 uptake to resume. Figure 2 shows similar data from the Roccarespampani site of coppiced Turkey oak (*Quercus cerris* L.) in Italy. Comparable data for two such precipitation events during summer on the Italian Island of Pianosa in the Tyrrhenian Sea are shown in Figure 3. This island was abandoned in 1988 and the former agricultural arable fields and pastures are reverting to the adjacent, surrounding macchia. The flux tower is centrally situated with a footprint that encompasses both the natural macchia vegetation and the old-field succession.

It is evident from the data for the three sites—sparse open forest with large trees and intervening pasture, a denser

Table 1. Site, stand and soil characteristics of the field sites at Roccarespampani and Mitra.

Variable	Roccarespampani, Italy	Mitra, Portugal
Site characteristics		
Main species	*Quercus cerris*	*Q. suber* and *Q. ilex*
Longitude	11°55′ E	8°00′ W
Latitude	42°24′ N	38°32′ N
Area of site (ha)	1250	700
Elevation (m)	120–160	243
Mean annual temperature (°C)	14	15.4 (3–31)
Mean annual rainfall (mm)	755	665
Stand characteristics		
Standing biomass (Mg ha^{-1})	32.1	n.a.
Leaf area index	1.40	0.55 tree, 1.8 herb/shrub
Tree diameter (cm)	4.9	38 ± 17 (*Q. ilex*)
Tree density (ha^{-1})	745	35–45
Tree height (m)	15	5
Amount of woody debris (Mg ha^{-1})	24	n.a.
Litter fall (g m^{-2})	75.6	n.a.
Rotation length/tree age (year^{-1})	15–20	80–90
Soil characteristics		
Soil type	Luvisol	Distric cambisol
Soil mineralogical class	Volcanic	Quartzodiorite/granodiorite
Soil depth (cm)	100	40
Root depth (cm)	50	500
pH	5.7	5.5
Total organic C (Mg ha^{-1})	90.9	12.8
Total N (Mg ha^{-1})	24.1	1.2
Bulk density (g cm^3)	1.22	1.7

coppiced forest with intervening sparse shrubs and herbs, and abandoned fields with surrounding macchia—that after a prolonged period of dryness, rainfall led within a few hours to large CO_2 emissions that were maintained for a few days be-fore declining to a low basal rate. Comparable results have now been obtained from many other similarly instrumented flux sites in both Mediterranean- and savannah-climate regions around the world.
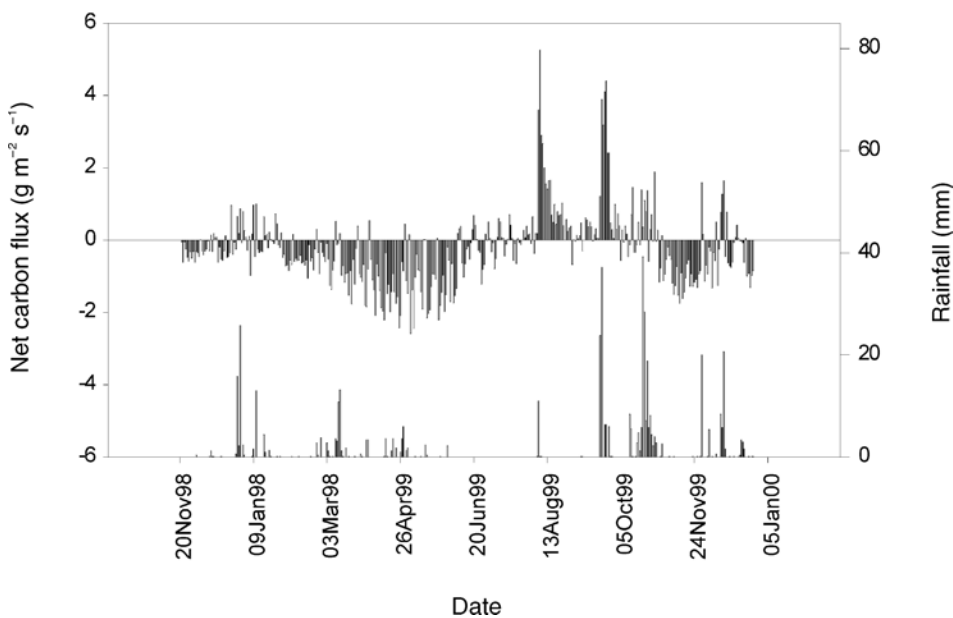

Figure 1. Seasonal course (November 1998–January 2000) of net ecosystem exchange of CO_2 measured by eddy covariance at the Mitra site, near Évora, Portugal. The dominant vegetation comprises scattered trees of cork oak (*Quercus suber*) and holm oak (*Q. ilex* ssp. *rotundifolia*). The upper part shows net daily carbon flux; the lower part shows daily total rainfall. (Data of M. Rayment, J. David and J. Pereira).
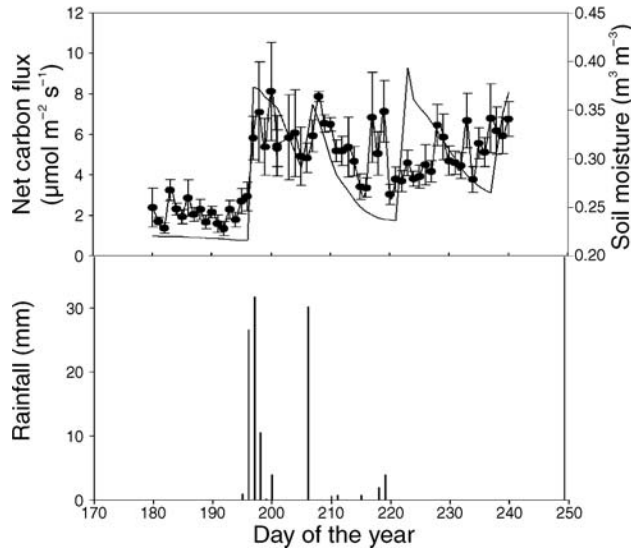
Figure 2. Seasonal course (2002) of net ecosystem exchange of CO_2 measured by eddy covariance in the recently coppiced stand at the Roccarespampani site in Italy. The dominant vegetation comprises scattered trees of Turkey oak (*Q. cerris*), 80% of which were coppiced two years previously. The upper part shows net daily carbon flux (●) and soil volumetric water content (solid line); the lower part shows daily precipitation. (Data of G. Manca, R. Valentini and M. Borghetti).

peratures and large water vapor saturation deficits, are characteristic of the Mediterranean climate and lead to hot and dry soils that are intermittently rewetted. These are similar to the conditions that were found some 45 years ago by Birch in the laboratory to lead to the stimulation of microbial-driven, enhanced decomposition and mineralization of soil organic matter (Appendix 1).

Field observations and experiments: plot scale

Soil CO_2 emission in response to a natural rainfall event

An automated soil respiration system with open chambers (Rayment and Jarvis 1997) was deployed at Mitra in six pasture plots (22×10 m) distributed among the trees. By adopting a system that continuously measures soil CO_2 efflux, volumetric soil water content and temperature, it was possible to track the CO_2 emission pulse from the soil surface. A typical time-series of CO_2 efflux from one of the chambers is shown in Figure 4, together with the environmental drivers, following a natural precipitation event of 18 mm within a 12-hour period at the end of the summer drought in 2004. The general shape of the response is described well by an exponential decay, very similar to that resulting from the experimental rewatering shown in Figure 5. The time taken for CO_2 efflux to return to

It is common knowledge that drought reduces leaf expansion and height growth of trees, causes stomatal closure and restricts photosynthesis, whereas alleviation of drought reverses these effects. It was, therefore, surprising to find that when it rained in summer on sites with Mediterranean or savannah climate there was almost immediately a large loss, not gain, of CO_2. Sporadic rainfall events, interspersed by dry periods often several weeks in duration, associated with high air tem-
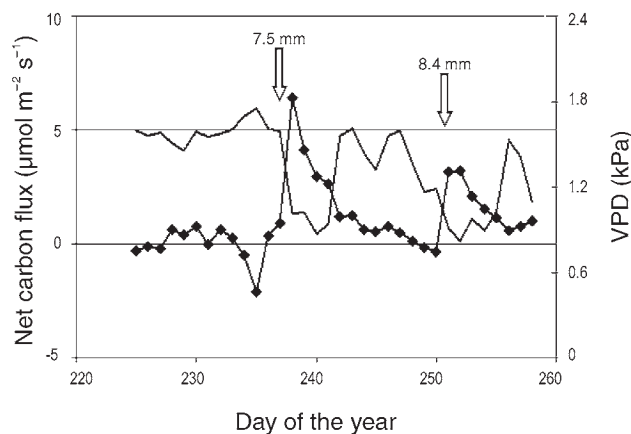

Figure 3. Seasonal course (2002) of net ecosystem exchange of CO_2 (◆), measured by eddy covariance, and atmospheric water vapor pressure deficit (VPD, plain line) at the center of the Isle of Pianosa in the Tyrrhenian Sea (18 nautical miles SW of Elba). The vegetation comprises macchia and abandoned (1988) agricultural croplands and pastures. (Data of F. Miglietta).
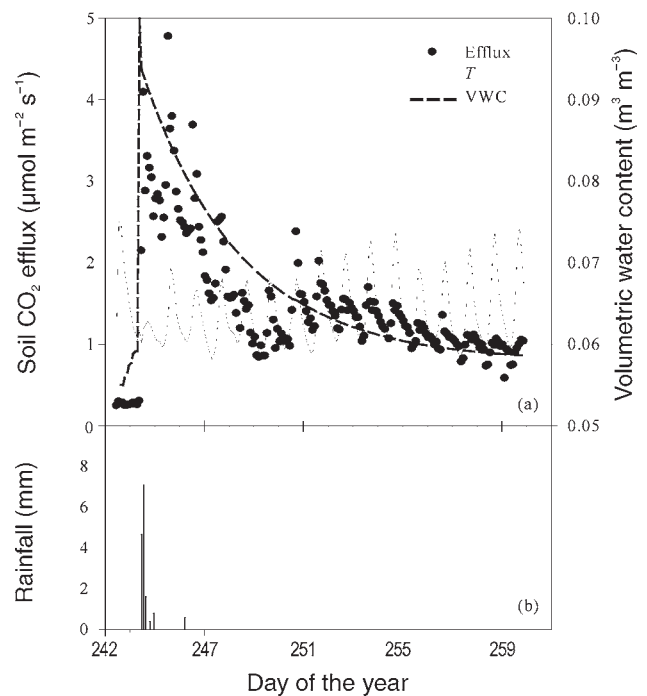

Figure 4. Effect of a natural 18-mm rainfall event on in situ soil CO_2 efflux) measured with a number of open, continuous-flow-through chambers on the soil surface near the Mitra site tower. Upper panel: the pulse of CO_2 efflux (●); the diurnal cycling of soil temperature (T; solid line); and the initial rise and subsequent decay in volumetric soil water content (VWC; dashed line). The lower panel shows precipitation events. (Data of L. Wingate, J. Banza, J. David and J. Pereira).
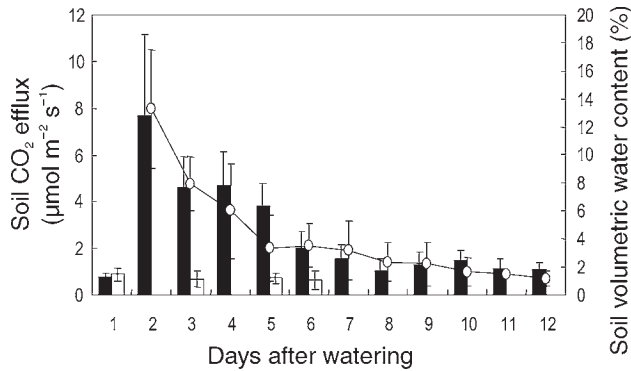
Figure 5. Effect of an experimental irrigation of field plots near the Mitra site tower on soil CO_2 efflux. Six 1.5-m-diameter plots, 10 m apart, were irrigated to field capacity in summer after a period of dryness before the onset of summer rains. Water was applied in three instalments over three days to avoid surface run-off. The open circles ($\bigcirc$, ± standard deviations) represent volumetric soil water content. Measurements of CO_2 emission (solid bars ± standard deviations) were made at four locations in each irrigated plot twice a day before and after the irrigation. The open bars (± standard deviations) represent the CO_2 efflux from the unirrigated soil. (Data of J.Banza, J. David and J. Pereira.)

the pre-rainfall rate was about 30 days. Because of the fine temporal resolution, it was possible to observe the daily temperature response of CO_2 efflux, superimposed on the overriding decay of the flux following the decline in soil volumetric water content. During the precipitation event there was a substantial drop in soil temperature of about 10 °C accompanied by a 15-fold increase in CO_2 efflux from ~0.26 to 4.1 μmol $m^{-2}\ s^{-1}$, similar to the enhancement observed in the experimentally rewetted plots. Once the rain and cloud cover had cleared the following day, both soil temperature and CO_2 efflux increased further, the latter peaking at ~5 μmol $m^{-2}\ s^{-1}$. Over the initial 10 days of the pulse (Figure 4), approximately 18 g C m^{-2} were lost.

Soil CO_2 emission response in experimentally rewetted field plots

Six pasture plots, 1.5 m in diameter and 10 m apart, near the Mitra eddy-flux tower were watered in the middle of summer. Four measurements of CO_2 emission were made in each plot with a portable closed dynamic chamber placed on the soil surface (EGM–1, PP-Systems, Hitchin, U.K.). The measurements were made in situ, twice per day, before and after watering the plots. In the middle of summer, before any summer rain, the dry soil in each plot was watered to its estimated field capacity. The watering was done in three instalments on consecutive days to avoid superficial runoff and any bias that might result from a temporary excess of water. Nine dry plots that were not irrigated served as controls. The results shown in Figure 5 demonstrate that rewetting the soil led to CO_2 emission and illustrate the magnitude and time course of this effect. The results following irrigation were quite similar to the response to the natural rainfall event shown in Figure 4.

Interaction between soil temperature and water content: plot scale

Effects of steady state temperature and moisture content on CO_2 emission from the forest floor

To enable modeling of soil respiration in relation to soil temperature and volumetric water content, emission of CO_2 was measured in nine, 30-m-diameter plots (to cover all tree density classes) at the Mitra site. Within each plot there were 16 measuring points distributed concentrically in three circles. Four measurements of CO_2 emission were made in each plot, twice a day, with a portable, closed dynamic chamber placed on the soil surface (EGM–1) and soil water at a depth of 15 cm was measured by time domain reflectometry. Estimates of the apparent respiration temperature coefficient (Q_{10}) were made following Davidson et al. (1998). There were no significant differences in mean respiration rates and Q_{10} between the replicate plots, but there were substantial significant differences when the data from within the plots were grouped with respect to soil water content, as shown in Figure 6.

Laboratory experiments

At the Roccarespampani site, the relationships between soil respiration rates, carbon mineralization rate, soil water content and temperature were determined in the field much as described above for the study at the Mitra site (Rey et al. 2002, Tedeschi et al. 2006). Additionally, measurements were made on soil samples collected from the site and incubated to target soil water contents at controlled soil temperatures in the laboratory (Rey et al. 2005, Rey and Jarvis 2006), with the aim of determining the interaction between mineralization rate and soil temperature and water content. Because these were steady state determinations, the experimental procedures were similar to those of Birch (Rey et al. 2005).

Interacting steady state effects of soil temperature and water content on mineralization rates

Soils from the topmost 0–5 cm soil layer were incubated at four temperatures: 4, 10, 20 and 30 °C and five water contents:
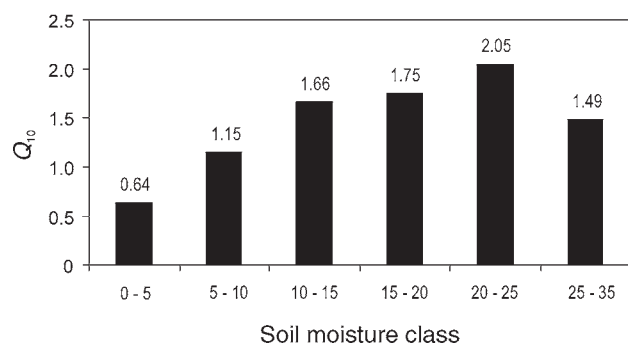

Figure 6. Apparent Q_{10} values calculated according to Davidson et al. (1998) for soil CO_2 efflux measured in situ in relation to soil temperature and soil water content on nine 30-m-diameter plots at 16 locations distributed concentrically in three circles at the Mitra site. (Data of J. Banza, J. David and J. Pereira).

20, 40, 60, 80 and 100% water-holding capacity (WHC) and the relationships between carbon mineralization rate, water content and temperature determined. In contrast to the Mitra field plots, the temperature sensitivity of mineralization was only weakly related to soil water with Q_{10} values of 3.21, 3.51, 3.34, 3.91 and 3.85 for the 100, 80, 60, 40 and 20% WHC treatments, respectively (for details see Rey et al. 2005). Based on these data, a multiple polynomial model was developed that predicted heterotrophic rates of respiration and carbon mineralization rates as a function of steady state soil temperature and water content ($R^2 > 0.99$, Figure 7).

Mineralization rate of rewetted soil over a range of water contents

The mineralization rate of soils incubated at different water contents 1 and 24 h after rewetting was investigated experimentally on soil samples from Roccarespampani (Rey et al. 2005). In all cases, there was a rapid response to sudden increases in water content. Figure 8 shows that the largest change was measured after 1 h and that the soils incubated at 60% WHC or less responded positively to a sudden increase in water content, with the largest increase in the 20% WHC treatment, and a negative response at a WHC greater than 60%.

The Birch effect at stand, plot and laboratory scales

Like Birch, we have observed the effect of experimental rewetting on a few hundred cm^3 of soil in laboratory incubation chambers. We have also observed the effect of rewetting by natural rainfall in the field, sampling 100 cm^2 to 1 m^2 with chambers on the forest floor, and with flux towers that sample
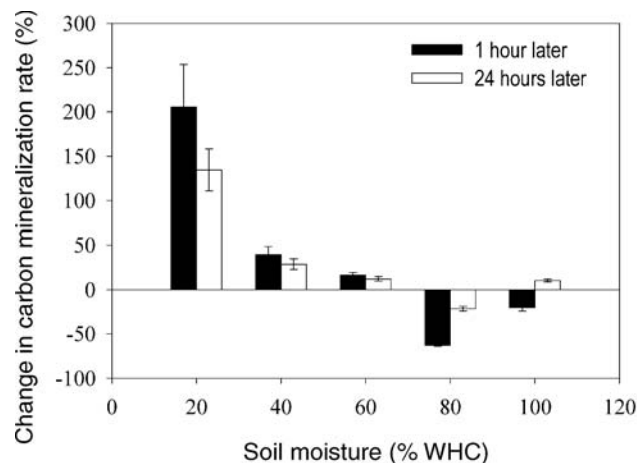
Figure 8. Effect of experimental rewetting in the laboratory of soil samples taken from the 0–5-cm mineral soil layer at the Roccarespampani site. Soil samples were pre-incubated to achieve five soil water contents. Percent change in carbon mineralization rates are shown 1 and 24 h after rewetting the soil samples to achieve a 20% increase in water content. The incubation temperature for the experiment was 25 °C. (Adapted from Rey et al. 2005).

CO_2-exchanges over a land area of 0.5 to 5 km^2. Furthermore, we have substantiated the effect in the field and in the laboratory by irrigation experiments. The results from the controlled rewetting field experiment and the controlled rewetting laboratory experiment indicate that sudden changes in soil water content can lead to enhanced CO_2 emission and increased mineralization, and complement the field observations of similar effects at both the stand and plot scales during the dry summer months. These results are consistent with the results obtained by Birch some 45 years earlier working on soils in the laboratory in a savannah climate region, and warrant the "Birch effect" attribution. Thus, it is reasonable to assume that the Birch effect as described by Birch (Appendix 1) and as observed in Mediterranean climate sites and soils, may be applicable to the extensive range of dryland ecosystems in regions with savannah and Mediterranean climates, and in other semi-arid regions.

Prediction of carbon mineralization rates in the field

There is a plethora of statistical and semi-empirical models relating soil respiration to soil temperature and water content in steady or semi-steady state conditions (e.g., Reichstein et al. 2002, 2003, Rey et al. 2005, Rey and Jarvis 2006), but at the present time, there is a dearth of mechanistic models appropriate for the unsteady conditions characteristic of the Birch effect. The polynomial model developed from the steady state incubation experiments, illustrated by the grid in Figure 7, was used to predict rates of heterotrophic soil respiration throughout a year. The main inputs were soil temperature and water content in the top 10 cm of soil. The effect of temperature was represented by the exponential Q_{10} function and the effect of water content by a linear function. The model worked rela-
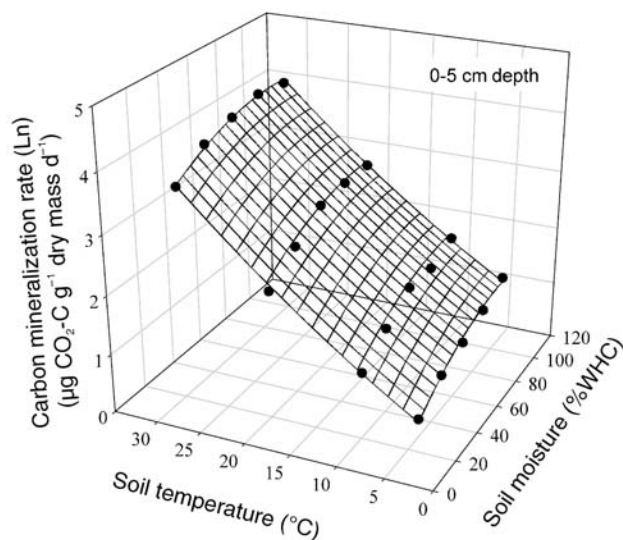

Figure 7. Steady state laboratory measurements (●) of carbon mineralization rates (log-transformed) in relation to temperature and water content of soil samples from the 0–5 cm mineral soil layer at the Roccarespampani site superimposed on a network of values modeled with a polynomial equation derived from the same dataset. (Adapted from Rey et al. 2005).

tively well for the steady state conditions in winter and during part of the autumn, but did not work at all well for the summer months for two reasons. First, the model overestimated heterotrophic soil respiration when soil temperatures exceeded 30 °C, and consequently were outside the range of determination of the temperature function. Second, the model underestimated the transient pulses of CO_2 emission stimulated by rainfall after dry periods. To deal with the first problem, we assumed that respiration did not increase with temperature above 30 °C. To deal with the second problem, we mimicked the effect of sporadic rainfall events during the summer months with a simple correction factor based on the sudden large changes in carbon mineralization rates that we had observed in the laboratory rewetting experiment. By these means, we improved the predictions so that the subsequent model, shown in Figure 9, reflected the high peaks in heterotrophic respiration observed in the field immediately after rainfall events ($r^2 > 0.81$, slope = 1.0 for the comparison between observed and predicted rates of soil respiration). However, although such an empirical approach emphasises the quantitative significance of the pulse for estimates of periodic CO_2 emissions, it does not enhance understanding of the processes involved, and is not a satisfactory basis for future predictions. To make further progress, a proper understanding is required of the processes leading to the pulses of nitrogen availability and CO_2 emission. In view of the contrasting hypotheses in current vogue, it may be some time before a process-based model can be realized.

Discussion

Understanding mineralization of soil organic matter

The results presented here demonstrate that soil water and temperature are important variables controlling mineralization and CO_2 emission rates in Mediterranean forest ecosystems, and that they predict heterotrophic rates of respiration in these soils during steady state periods. Moreover, the results suggest that sudden increases in soil water after drought can considerably increase soil CO_2 efflux, most likely because of increased soil heterotrophic respiration as a result of stimulation of microbial activity.

As we have shown, models parameterized using steady state data typically underestimate the magnitude of CO_2 efflux because of the pulse of CO_2 efflux that follows soil rewetting. Consequently, we either under- or overestimate CO_2 fluxes during dry periods. Soil water and temperature data alone cannot provide an explanation of the mechanism for enhanced CO_2 release during transient rainfall events. However, by taking account of the relative change in soil water content during the pulse, we could improve predictions of CO_2 efflux during these transient events. Several studies have shown that microbial water stress is not only a function of the absolute value of soil water potential, but also depends on the scale of change in water potential (Kieft et al., 1987). For example, Orchard and Cook (1983) found a linear relationship between the magnitude of change in water potential when a dry soil is wetted and the size of the resultant CO_2 pulse.
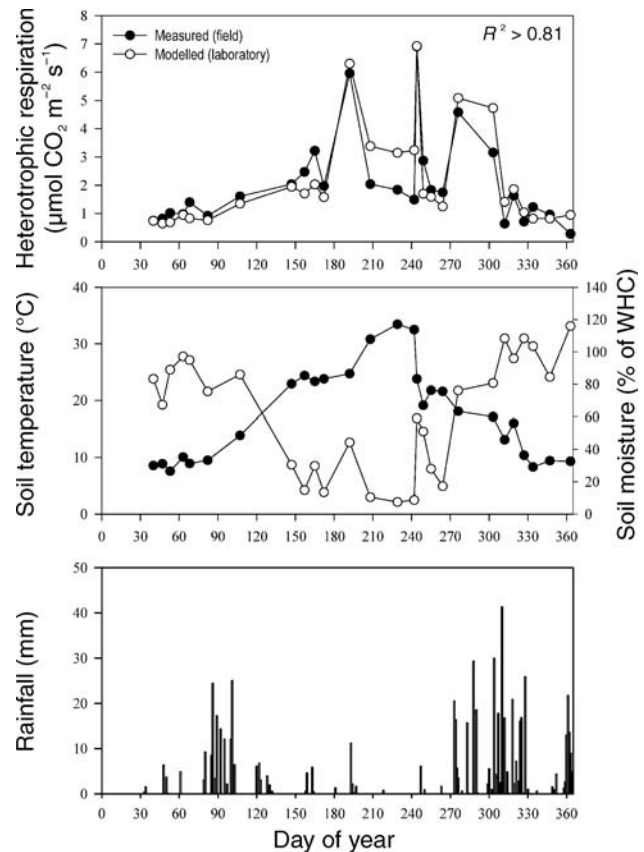

Figure 9. Testing the model in the field against field data for the year 2000 at the Roccarespampani site. Uppermost panel: predicted soil mineralization rates (○) compared with measured rates of soil heterotrophic respiration in the field (●). The predicted soil mineralization rates are based on the empirical model and model parameters obtained from the laboratory measurements (from Rey et al. 2005), and using the measured annual course of soil temperature (●) and soil volumetric water content (○) (middle panel), and daily precipitation (lowermost panel). The measured rates of soil heterotrophic respiration in the field were obtained with the EGM system on trenched plots from which roots, leaf and branch litter were excluded (see Rey et al. 2002).

Several mechanisms have been proposed to explain the observations of increased C and N cycling on rewetting of the soil. Birch attributed the enhanced mineralization, in part, to a rapid, immediate explosion in microbial populations, particularly in the organic surface soil layers, together with structural alterations in soil macro and micro-aggregates (Griffiths and Birch 1961). However, evidence is now accumulating in support of an alternative hypothesis that the CO_2 pulse results from an osmotic shock to the populations of soil microbes. One possible scenario, for which there is considerable support from ^{14}C labeling of microbial populations and soils in laboratory studies (e.g., Fierer and Schimel 2003), is as follows. During periods of drought, compatible solutes rich in carbon and nitrogen (e.g., sugars, aminoacids, betaines) accumulate in the cytoplasm of the microbes and fungi, thereby resisting cell desiccation. When rain falls, diluting the remaining soil solution, microbes take up water, increasing in volume and turgor

pressure, which leads to release or expulsion of some of the cytoplasmic solutes into the soil solution. Through this mechanism, bacteria and fungi are almost instantaneously able to raise their intracellular water potentials and so avoid osmotic stress and lysis. Within as little, perhaps, as 10 minutes, a new water potential equilibrium is established and the microbial cells begin to reabsorb and release metabolites, generating CO_2 through the associated respiration, and producing an almost immediate, transient, gaseous pulse of CO_2, NO and N_2O (Halverson et al. 2000, Sleator and Hill 2001, Fierer and Schimel 2003).

The largest change in CO_2 emission shown in Figure 9 was in soils incubated at the lowest water contents and the pulse was largest one hour after the change in water content, consistent with the hypothesis described above. Thus, incorporation of concurrent measurements of changes in soil volumetric water content, or soil water potential, should provide a better explanation of CO_2 emission data collected at larger scales in the field. Because the change in soil water potential is likely to relate to the size of the rewetting event, this should lead to improvements in predictions of responses of both soil and ecosystem respiration to variability in the size and frequency of precipitation events. For instance, Xu et al. (2004) found a positive linear relationship at the ecosystem scale between the amount of precipitation and the total carbon respired from the understory of a woodland and grassland ecosystem in the Mediterranean climate of California.

Impact of the Birch effect on annual carbon balances

In most, if not all, annual daily patterns of NEE over a wide range of climates, there are days on which there is a net return of CO_2 to the atmosphere over a period of 24 h. In boreal forests, these are frequently days in autumn with short photoperiods, and days during the winter freeze-up (Black et al. 2005). In evergreen temperate forests, these may be days of extreme cloudiness and rain, particularly in autumn and spring when days are short (Clement et al. 2003). In deciduous temperate forests, small daily losses of carbon accumulate over the leafless winter (Malhi et al. 1999, Clement et al. 2003, Baldocchi and Xu 2005).

The eddy-covariance data shown here, and also by Xu et al. (2004), demonstrate that days on which carbon is returned to the atmosphere can be frequent in forests and macchia in Mediterranean climate regions during times of summer drought as a result of drying and rewetting of soils by sporadic rainfall. In both boreal and temperate forests, extended droughts are by comparison uncommon, and in general, the soils remain moist so that the Birch effect does not occur. However, the Birch effect has been observed during extended summer droughts in some temperate forest ecosystems (e.g., Tang et al. 2005).

Quantitatively, do these emissions of CO_2 and N_2O to the atmosphere matter? To answer that question, we should consider the impacts from the perspective of the vegetation, the soil and the atmosphere, and in doing so, we should take associated feedbacks into account.

Vegetation Figure 9 shows that the short-term consequence of the Birch effect is to reduce the annual net ecosystem gain of carbon. However, the accelerated release of nitrate and other nutrients and increased water availability is likely to promote vegetation growth, providing it can compete for the resources. For instance, soil microbes may be active at times when plants are not, thereby increasing immobilization of mineral nutrients in microbial biomass (Singh et al. 1989, Bolton et al. 1993, Austin et al. 2004). Thus, taking a longer-term view, the associated mobilization of nitrogen and other nutrients is likely to stimulate higher net primary productivity (NPP), thus enhancing carbon storage within vegetation, i.e., mineralization and release of nutrients may provide a significant compensating feedback. This is likely to be of particular significance for vegetation that is chronically deficient in nitrogen. However, this response depends on a degree of synchrony between the nutrient pulses and the capacity of the vegetation to respond to them. For instance, should drought periods become longer and the frequency of small rainfall events increase, the capacity of vegetation to exploit transiently available nutrients during periods of limited water availability could be severely constrained, possibly leading to a larger efflux of CO_2, NO and N_2O to the atmosphere.

Soil The influence of the Birch effect on carbon cycling depends on vegetation, soil type and microbial community dynamics. For example, in the short-term, multiple drying–rewetting events can result in moderate increases in respiration rates of soils under oak vegetation, whereas soil respiration rates under grassland tend to decrease after multiple rewetting cycles (Fierer and Schimel 2002). On longer time scales, the influence of this stress history is detectable up to six weeks after the last stress cycle, indicating that soils do not return to the same equilibrium respiration rates, most likely because of changes in the microbial communities. This suggests that long-term rates of soil carbon mineralization may be substantially lowered by a high degree of variability in soil water content (Fierer and Schimel, 2002).

Atmosphere Inputs of CO_2 and N_2O to the atmosphere must be regarded as particularly deleterious at the present time. It is a crucial feature of the Birch effect, as we now perceive it, that more CO_2 is emitted to the atmosphere from a succession of drying–rewetting events than if the soil remains moist. Although the pulses of CO_2 emission resulting from the Birch effect are short-lived, when integrated over time they make a significant addition to the return-flux of CO_2 to the atmosphere, and consequently reduce the annual net gain of carbon by vegetation (Figure 10). We must also take into account corresponding increases of N_2O, which has a global warming potential of about 290 times that of CO_2 (IPCC 2001).

The total area of lands with Mediterranean and savannah climates (30–35 million km^2) approximates the global areas of wet and moist tropical forests, temperate forests and boreal forests combined. These global forests are the terrestrial power-house for atmospheric CO_2 removal, and they contain the major reservoirs of global ecosystem carbon in their soils
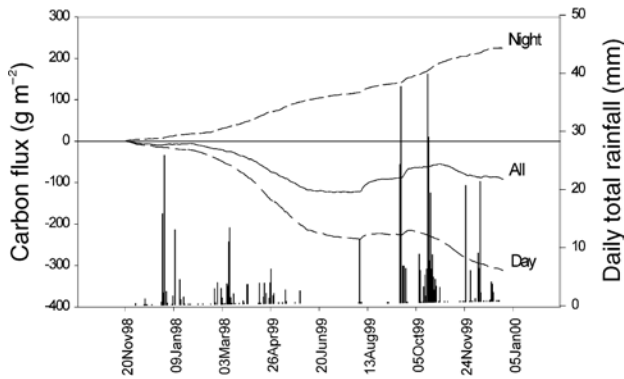
Figure 10. Cumulative annual course of net ecosystem carbon flux measured by eddy-covariance at the Mitra site. The data in Figure 1 are plotted cumulatively to show the effect of CO_2 emissions stimulated by rainfall on the accumulation of carbon over the year. The reductions in slope of the accumulated total carbon gain show that rain-stimulated CO_2 emission has an appreciable effect on annual carbon sequestration. (Data of M. Rayment, J. David and J. Pereira).

(Dixon et al. 1994, Schlesinger 1997). Additionally, N_2O emissions from the soils of these forests are small, apart from poorly drained and flooded areas (Brumme et al. 2005). If climate change should increase the global extent of areas with Mediterranean and savannah climates at the expense of the temperate and tropical forests, CO_2 removal from the atmosphere is likely to be reduced, and CO_2 and N_2O emissions to the atmosphere may be increased. We conclude that a full greenhouse gas inventory of the quantitative contributions of the Birch effect (CO_2 and N_2O emissions), for all of the global semi-arid land areas, is desirable.

Acknowledgments

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Appendix I

Short CV of H.F. Birch (born 1912; died 1982)

1931–34. B.Sc. 1st Class Honors, Chemistry and Physics, Liverpool University

1934–37. Ph.D. Synthesis of Natural Products, Liverpool University

1937–38. Research Assistant, Liverpool University

1938–41. Cacao Biochemist, Imperial College of Tropical Agriculture, Trinidad

1941–45. Agricultural Chemist, Dept of Agriculture, Jamaica

1945–48. Biochemist Cinchona Research Organisation, Tanganyika; extraction of alkaloids, especially quinine, from cinchona tree bark

1948–61. Head of Agricultural Chemistry and Soils Department, *East African Agricultural and Forestry Research Organisation* (EAAFRO, Director Charles Pereira), Muguga, near Nairobi, Kenya

1961–65. Professor of Soil Science and Agricultural Chemistry, Makerere University, Kampala, Uganda

1965–71. FAO Consultant on soil fertility and low yields, Ethiopia

1971. Retired from FAO; resigned from British Society of Soil Science (diabetes, causing failing eyesight)

33 journal publications (10 in *Nature*)

Reports to the Colonial Office and FAO

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