

Breeding crop plants with deep roots: their role in sustainable carbon, nutrient and water sequestration

Douglas B. Kell^{1,2,*}

¹School of Chemistry and Manchester Interdisciplinary Biocentre, University of Manchester, 131 Princess Street, Manchester M1 7DN, UK and ²Biotechnology and Biological Sciences Research Council, Polaris House, North Star Avenue, Swindon SN2 1UH, UK

*For correspondence. E-mail dbk@manchester.ac.uk

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- **Background** The soil represents a reservoir that contains at least twice as much carbon as does the atmosphere, yet (apart from 'root crops') mainly just the above-ground plant biomass is harvested in agriculture, and plant photosynthesis represents the effective origin of the overwhelming bulk of soil carbon. However, present estimates of the carbon sequestration potential of soils are based more on what is happening now than what might be changed by active agricultural intervention, and tend to concentrate only on the first metre of soil depth.
- **Scope** Breeding crop plants with deeper and bushy root ecosystems could simultaneously improve both the soil structure and its steady-state carbon, water and nutrient retention, as well as sustainable plant yields. The carbon that can be sequestered in the steady state by increasing the rooting depths of crop plants and grasses from, say, 1 m to 2 m depends significantly on its lifetime(s) in different molecular forms in the soil, but calculations (<http://dbkgroup.org/carbonsequestration/rootssystem.html>) suggest that this breeding strategy could have a hugely beneficial effect in stabilizing atmospheric CO₂. This sets an important research agenda, and the breeding of plants with improved and deep rooting habits and architectures is a goal well worth pursuing.

Key words: Breeding, deep roots, genetics, root architecture, carbon sequestration, nutrient efficiency, drought resistance, soil structure, perenniality.

INTRODUCTION

Whatever the extent and dynamics of increased levels of atmospheric CO₂ [and of other greenhouse gases (GHGs), for which similar arguments apply], the greenhouse effect means that temperatures will rise monotonically with their levels. A precautionary principle seeks to stop these increases of GHGs, or even to lower them in the steady state. While this may in part be effected via lowered emissions, a major role is to be played by mechanisms that extract CO₂ from the atmosphere and sequester it in the earth or oceans for a greater or lesser period. Oceans contain approx. 50 or more times the CO₂ than does the atmosphere (Smith, 2004; MacKay, 2008), but increased dissolution of atmospheric CO₂ in oceans (and lakes) leads to their further acidification, with many undesirable consequences (Sabine *et al.*, 2004; Orr *et al.*, 2005; Riebesell *et al.*, 2007; Hall-Spencer *et al.*, 2008; McNeil and Matear, 2008; Reid *et al.*, 2009; Doney, 2010; Shi *et al.*, 2010; Turley *et al.*, 2010). Unless marine carbon storage could be effected in a recalcitrant form that sinks rapidly (Jiao *et al.*, 2010; Stone, 2010; Jiao and Azam, 2011), this implies that CO₂ should probably best be sequestered elsewhere if we are to have ecosystems in which the net ecosystem carbon budget (Chapin *et al.*, 2006; Smith *et al.*, 2010b) is accumulative.

Terrestrial and marine environments presently absorb about half the anthropogenic CO₂ (Schimel *et al.*, 2001), and soil contains at least twice the amount of carbon than is in the atmosphere (Batjes, 1996) (and three times that in vegetation

(Smith, 2004), with enormous if uncertain fluxes in both directions (Jackson *et al.*, 1997; Post and Kwon, 2000; Meir *et al.*, 2006; Reay *et al.*, 2007; MacKay, 2008; Philippot *et al.*, 2009; Prechtel *et al.*, 2009; Bond-Lamberty and Thomson, 2010; Crevoisier *et al.*, 2010; Eglin *et al.*, 2010; Macías and Arbestain, 2010; Smith and Fang, 2010; Singh *et al.*, 2010; Bastviken *et al.*, 2011) (that are nevertheless quite small relative to the pools; Smith, 2004). Thus, increasing soil carbon in the steady state by just 15 % would lower atmospheric CO₂ by 30 %, offering a huge environmental benefit. In addition, there are indications (Bellamy *et al.*, 2005; Monson *et al.*, 2006; Luo, 2007; Arnone *et al.*, 2008; Bond-Lamberty and Thomson, 2010; Smith and Fang, 2010; Yvon-Durocher *et al.*, 2010; Zhao and Running, 2010) of a positive feedback in which increases in global temperature lower the ability of present soils and other parts of the biosphere to absorb CO₂, so clearly some kind of intervention is needed. This implies changes in agricultural practice (Robertson *et al.*, 2000; Lal, 2004, 2008a, b, 2011; Sartori *et al.*, 2006; Pretty, 2008; Smith *et al.*, 2008; Burney *et al.*, 2010; Follett and Reed, 2010; Smith and Olesen, 2010; Powlson *et al.*, 2011), in an environment in which edible crop yields also need to increase substantially and sustainably (Beddington, 2010; Fedoroff *et al.*, 2010; Godfray *et al.*, 2010a, b; Lal, 2010c; Pretty *et al.*, 2010; Tester and Langridge, 2010; Foresight, 2011), and where transport fuels and organic chemicals will need to come from modern (rather than fossil) photosynthesis (e.g. Bozell and Petersen, 2010; Somerville *et al.*, 2010;

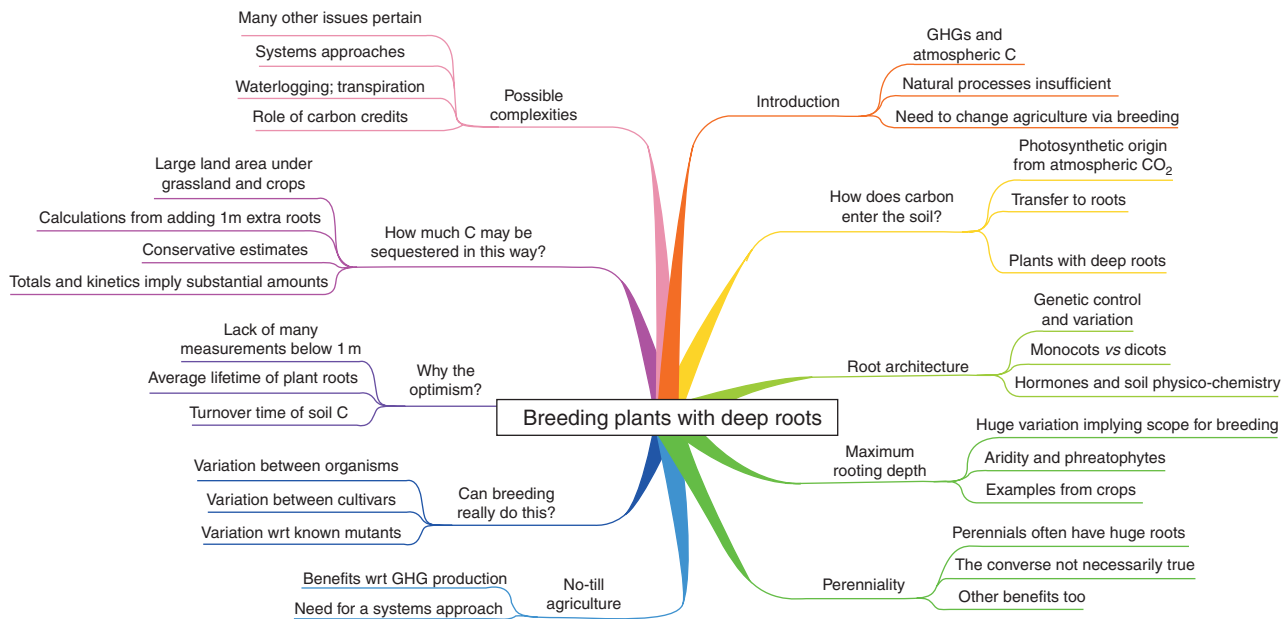


FIG 1. A mind map (Buzan, 2002) summarizing the content of this review. To interpret this, start at the top and read clockwise.

Vispute *et al.*, 2010; Whited *et al.*, 2010; Demirbas, 2011). The purpose of this review, as summarized in Fig 1, is to develop the relevant arguments.

Certainly it is recognized that the substantial (possibly 10- or even 20-fold) decreases in atmospheric CO₂ over geological time, especially during the Devonian (416.0–359.2 Ma) and more gradually since the Cretaceous (145.5–65.5 Ma), have largely been effected via the production of deep-rooted trees and the rise of angiosperms, respectively (Mora *et al.*, 1996; Berner, 1997; Berner and Kothavala, 2001; Royer *et al.*, 2001; Taylor *et al.*, 2009). These facts provide an important guide to what may be possible, since the kinds of decreases being needed now are rather lower (cf. Breecker *et al.*, 2010), and the role of plants (both roots and shoots) in effecting these decreases has historically been paramount. Note too that soil production can be much slower than its erosion without intervention (Torn *et al.*, 1997; Montgomery, 2007; Huggins and Reganold, 2008), and that roots lower erosion considerably (Gyssels *et al.*, 2005).

The required changes in agricultural practice, plus the existence of proof that carbon was indeed once highly sequestered in plant biomass, led to the recognition that increasing the amount of below-ground biomass en route to sequestering atmospheric CO₂ is a desirable goal. The purpose of this review is to point out not only that it is desirable but that it is possible, and to highlight the areas where research activities might usefully be focused.

HOW DOES CARBON ENTER THE SOIL?

Although atmospheric CO₂ can of course dissolve in soil moisture, and some carbon comes from manuring (Smith *et al.*, 2010b), these amounts are comparatively small and the chief initial method of carbon transfer to soil is via recent photosynthesis and subsequent transfer to plant roots (Jiménez and Lal, 2006; De Deyn *et al.*, 2008; Taylor *et al.*,

2009; Orwin *et al.*, 2010) and thence to soil organic matter (Kögel-Knabner, 2002). The first thing to note is the huge variation in the organic (carbon) content of soils – at least 15-fold in the UK alone (Bellamy *et al.*, 2005; Bradley *et al.*, 2005; Ostle *et al.*, 2009). This immediately indicates the large scope for increasing it in many places; indeed, the root content of different soils also varies at least 10-fold (Jackson *et al.*, 1996; Schenk and Jackson, 2002a), with a large variation in the vertical distribution of carbon (Jobbágy and Jackson, 2000). The magnitude and similarity of these factors (10- and 15-fold) might be taken to imply that variation in the amounts of roots themselves (rather than their exudates and soil biota, for instance) is likely to be the major cause of the variance, but clearly all processes relevant to both incorporation and decomposition (whose difference determines net values) can contribute to this variance. Given relevant data, inferencing methods (e.g. Pearl, 2000; Rohr *et al.*, 2008) can determine which processes drive which.

The soil ecosystem is extremely complex (e.g. Fitter *et al.*, 2005; Nielsen *et al.*, 2011), but a major role in sequestration of carbon secreted from roots (‘exudate’) is played by arbuscular mycorrhiza (AM) (e.g. Staddon and Fitter, 1998; Strack *et al.*, 2003; Zhu and Miller, 2003; Peterson *et al.*, 2004; Rillig, 2004; Parniske, 2008; Varma, 2008; Bucher *et al.*, 2009; Lambers *et al.*, 2009; Leigh *et al.*, 2009; Wilson *et al.*, 2009) with the roots of the majority of land plants. The mycorrhizal fungi (of the genus Glomeromycota) provide nutrients, especially phosphate (Bucher, 2007), to the plants, which in turn provide up to 20% of the carbon that they fix to the soil-dwelling fungal partners. Mycorrhiza also secrete a protein called glomalin (Gadkar and Rillig, 2006), whose extent correlates extremely well with desirable (large aggregates in) soil structure (Bedini *et al.*, 2009; Wilson *et al.*, 2009). The rhizosphere, as the interface between plants and soil, is clearly crucial. Roots, mycorrhiza and soil organic

carbon (SOC) can all affect each other beneficially, and the interactions are complex (Feeney *et al.*, 2006; O'Donnell *et al.*, 2007; Gillespie *et al.*, 2009; Hinsinger *et al.*, 2009; Lambers *et al.*, 2009; Luster *et al.*, 2009). A couple of examples include the facts that the soil biota (and roots) help increase the porosity of soil (Feeney *et al.*, 2006) and that roots both affect the physical architecture of soils and vice versa (Hinsinger *et al.*, 2009). However, since there is no unitary explanation of which processes dominate where, for present purposes I deem it sufficient to note the role of AM in these processes, and that the breeding strategies that this article seeks to promote should take their important activities into account. Experimental approaches may need to start by studying the covariation between root architectures and mycorrhiza, en route to performing experiments in which one is changed as an independent variable.

Several relevant areas of the literature are thus bound up with each other, albeit (as in most fields; e.g. Hull *et al.*, 2008; Dobson and Kell, 2008; Kell, 2009) that they have developed independently (the balkanization of the literature into 'silos'). Bringing them together indicates that the goal of breeding plants with extended root systems that can effect carbon, water and nutrient sequestration (Fig. 2) is not only desirable but attainable. Four particular scientific areas that pertain are root architecture and depth, perenniality and low- or no-till agriculture.

Root architecture

A number of papers and reviews describe the genetic control of root architecture (e.g. Zhang and Forde, 1998; Casimiro *et al.*, 2003; Hu *et al.*, 2003; Hochholdinger *et al.*, 2004a; Swarup *et al.*, 2005; Chaitra *et al.*, 2006; de Dorlodot *et al.*, 2007; Galinha *et al.*, 2007; Courtois *et al.*, 2009;

Hochholdinger, 2009; Hochholdinger and Tuberosa, 2009; Péret *et al.*, 2009; Benfey *et al.*, 2010; Bennett and Scheres, 2010; Coudert *et al.*, 2010; Iyer-Pascuzzi *et al.*, 2010; Paschold *et al.*, 2010; Yang *et al.*, 2010; Yi *et al.*, 2010; Zimmermann *et al.*, 2010; Lucas *et al.*, 2011). Thus, a number of root architecture genes are known via the effects of their mutations on traits such as primary root length, root branching, root hair formation, and so on, but our present knowledge of them all, and the mechanistic details by which they affect phenotype, is comparatively limited. Important features of the genetic control differ, for example (Gregory, 2006) between monocots (such as grasses, cereals and *Brachypodium distachyon*; Draper *et al.*, 2001) and dicots (such as *Arabidopsis thaliana*; Hochholdinger *et al.*, 2004a; Osmont *et al.*, 2007; Watt *et al.*, 2009; Zimmermann *et al.*, 2010) [and interestingly *B. distachyon*, unlike *A. thaliana*, forms associations with mycorrhiza (Bevan *et al.*, 2010)]. The very interesting ecological and evolutionary analyses that pertain (e.g. Fitter, 1987) are outside the scope of this summary, but can clearly provide very useful pointers to the breeding of plants with the desirable rooting traits that are highlighted herein. The chief of these is of course root depth.

As well as genetic means, root architecture is also controlled by hormonal influences from both the host plant (e.g. Tanimoto, 2005; Santner *et al.*, 2009) and soil organisms (see above), and to some degree by the physico-chemical environment (e.g. Fitter and Stickland, 1991; Cahill *et al.*, 2010). Our focus here, however, is on the genetic control, which seems to be dominant (Kato *et al.*, 2006).

Maximum rooting depth

There is considerable variation between both plant types and individual plant strains (cultivars) as to the maximum depth to

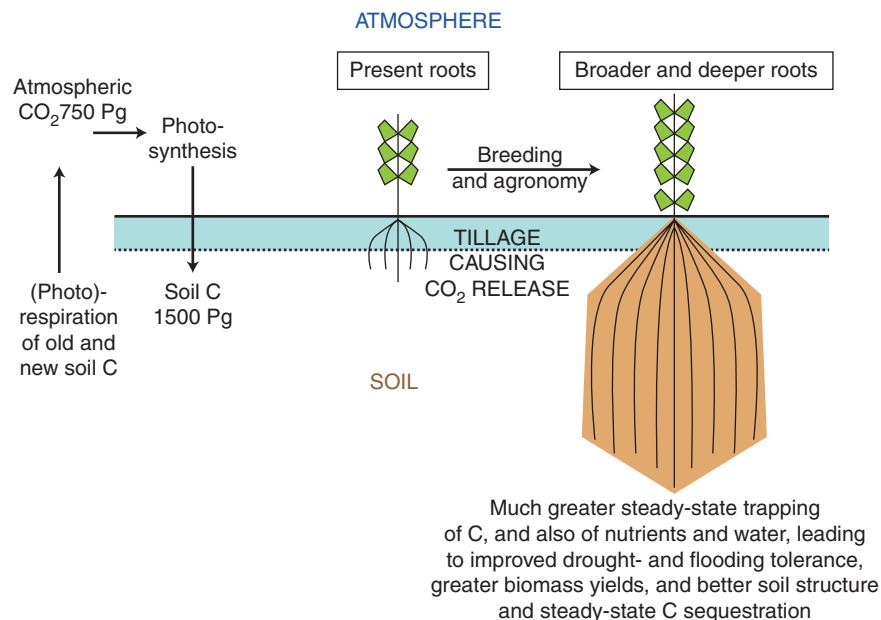


FIG. 2. Cartoon illustration of the potential for the improvement of agricultural and ecological traits by breeding crop plants with large root systems. The root morphologies are to be considered as illustrative only, and all details of bidirectional fluxes to and from litter and the many soil carbon pools (and including leaching and erosion) are omitted for clarity. For a summary of the various terms used to describe the most important carbon fluxes and stocks see, for example, Chapin *et al.* (2006) and Smith *et al.* (2010b).

which they are known to produce roots, but 2 m for angiosperms (and much more for trees) is not at all uncommon (Stone and Kalisz, 1991; Canadell *et al.*, 1996; Jackson *et al.*, 1996; Schenk and Jackson, 2002a, b; Hu *et al.*, 2003), implying equally that there is considerable scope for increasing the depth of roots by appropriate breeding strategies. A chief point to note is that most presently cultivated agricultural crops have root depths that indeed do not extend much beyond 1 m, albeit that a number do (Kristensen and Thorup-Kristensen, 2004; Kutschera *et al.*, 2009), such that this implies that there is indeed exceptional scope to breed this trait. (We recognize of course that many modern grains have been bred to have short stems, and with little or no attention being directed specifically to their roots.)

Root length is also typically a function of aridity (Canadell *et al.*, 1996; Schenk and Jackson, 2002a, 2005). Some very long-rooted plants, common in arid zones, are known as phreatophytes (Pataki *et al.*, 2008), although this term relates more to the fact that they obtain their water from deep sources. Root water dynamics in soil seem not to be as well understood as one would wish, as many mechanisms contribute, even to its sign (Burgess and Bleby, 2006) (i.e. whether plants add water to the soil or extract it from it), a phenomenon known as hydraulic redistribution (Burgess *et al.*, 1998). As well as the benefits to carbon sequestration, there is evidence supporting the role of roots in improving soil structure (Gregory *et al.*, 2010), on improving hydrology (Macleod *et al.*, 2007) and in showing that SOC improves agronomic productivity (Lal, 2010b). Some genes [or at least quantitative trait loci (QTLs)] improve both root architecture and plant yield (Passioura, 1983, 2006; Tuberosa *et al.*, 2002; Steele *et al.*, 2006, 2007; Hund *et al.*, 2007), and there are a number of examples of crops in which the below-ground biomass does contribute significantly to SOC (sequestration), including plants such as *Andropogon gayanus* (Fisher *et al.*, 1994), *Miscanthus × giganteus* (Clifton-Brown *et al.*, 2007; Heaton *et al.*, 2008; Dohleman and Long, 2009; Dondini *et al.*, 2009a, b; Hillier *et al.*, 2009), *Panicum virgatum* (switchgrass) (Ma *et al.*, 2000, 2001; Liebig *et al.*, 2005; Al-Kaisi and Grote, 2007; Anderson-Teixeira *et al.*, 2009; Collins *et al.*, 2010) and vetiver (*Chrysopogon zizanioides* L.) (Grimshaw, 2008; Lavania and Lavania, 2009) grasses, and even sugar cane (Otto *et al.*, 2009; Galdos *et al.*, 2010). At least five widely cultivated crop plants can produce roots exceeding 2 m (Kutschera *et al.*, 2009).

Perenniality

Perenniality, the use of crops that produce edible parts such as grains (seeds) without annual sowing (and ploughing), has been championed as an especially valuable idea for consideration, and this coheres significantly with the present theme. This is not least because such perennials typically develop considerably longer roots than do modern domesticated annual crops (Cox *et al.*, 2002, 2006; DeHaan *et al.*, 2005; Glover *et al.*, 2007, 2010; Dohleman and Long, 2009; DuPont *et al.*, 2010; Van Tassel *et al.*, 2010). Such perennials are also known to exhibit hugely decreased nitrate runoff (Randall and Mulla, 2001) and, importantly, to sequester much more carbon in soil (Robertson *et al.*, 2000; Kardol

and Wardle, 2010). The extent to which perenniality and these large root architectures can be decoupled, and whether and when this is desirable for agronomic purposes, remain uncertain, though at least some flowering time genes that contribute to perenniality seem to be conserved between monocots and dicots (Wang *et al.*, 2009; Higgins *et al.*, 2010), in a way that root architecture is not (see above). Consequently, it would seem that perenniality – though probably helpful – is not a necessary accompaniment to crop plants with deep roots.

No-till agriculture

Ploughing releases SOC and, in a similar vein, no-till agriculture (that may also be used with perennial crops) assists carbon sequestration and decreases soil erosion (e.g. Paustian *et al.*, 2000; West and Post, 2002; Sainju *et al.*, 2003; Lal *et al.*, 2004; Bernacchi *et al.*, 2005; Amado *et al.*, 2006; Montgomery, 2007; Huggins and Reganold, 2008; Villamil *et al.*, 2008; López-Bellido *et al.*, 2010), although tillage of surface layers that do not disturb deeper roots becomes at least partially a no-till process (see also Fig. 2). This said, though, it is important to analyse the entire system of GHG production to assess the detailed benefits of a more widespread no-till strategy (Robertson *et al.*, 2000; Six *et al.*, 2002; Grandy *et al.*, 2006; Steinbach and Alvarez, 2006).

CAN BREEDING REALLY DO THIS?

There are, of course, many examples (e.g. Lippman and Tanksley, 2001; Hill, 2005; Edgerton, 2009; Johansson *et al.*, 2010) that show the huge variation in phenotype achievable in agricultural breeding populations, and this is being stimulated further by techniques such as marker-assisted selection and genome-driven breeding (e.g. Moreau *et al.*, 2000; Meuwissen *et al.*, 2001; Eathington *et al.*, 2007; Collard and Mackill, 2008; Utomo and Linscombe, 2009; Kean, 2010; Meuwissen and Goddard, 2010). Nonetheless, it might be argued that the role of genetics or plant breeding in increasing root depth is likely to be negligible, and that (leaving aside soils with rock strata just below the surface, where this might be true) the depth of roots is governed entirely by the physico-chemical properties of the soil, and not at all by the genetics of the host (or soil organisms). The experimental facts are against this (Doussan *et al.*, 2003; Kato *et al.*, 2006), and a number of simple gene-based arguments show that this is not the case.

- (1) Plant root depths vary greatly in the same soil for different organisms (e.g. Burch and Johns, 1978; Jackson *et al.*, 1996; Jobbágy and Jackson, 2000).
- (2) Plant root depths vary substantially in the same soils or growth media for different cultivars of the same plant (e.g. O'Toole and Bland, 1987; Lilley and Fukai, 1994; Champoux *et al.*, 1995; Fukai and Cooper, 1995; Price *et al.*, 1997, 2002a, b; Angadi and Entz, 2002; Bonos *et al.*, 2004; Løes and Gahoonia, 2004; Chloupek *et al.*, 2006; Kato *et al.*, 2006; Devaiah *et al.*, 2007; Hund *et al.*, 2007, 2009, 2011; Sanguineti *et al.*, 2007; Kamoshita *et al.*, 2008; Karcher *et al.*, 2008; Crush *et al.*, 2009, 2010; Gregory *et al.*, 2009; Hargreaves

et al., 2009; Kutschera *et al.*, 2009; Trachsel *et al.*, 2009, 2011; Ao *et al.*, 2010; Iyer-Pascuzzi *et al.*, 2010; Obara *et al.*, 2010; Tuberosa *et al.*, 2010; Bayuelo-Jiménez *et al.*, 2011).

- (3) Plant root depths can vary substantially between different mutants (in known genes) of the same parent (e.g. Zhang and Forde, 1998; Casimiro *et al.*, 2003; Hochholdinger *et al.*, 2004*a, b*; Hochholdinger, 2009; Hochholdinger and Tuberosa, 2009; Rebouillat *et al.*, 2009; Benfey *et al.*, 2010; Coudert *et al.*, 2010).

Thus any claim that it is impossible to pursue the 'deep roots' agenda using plant breeding methods is without merit.

Why the optimism?

It is certainly the case that a number of experts have given a slightly less optimistic view of the potential of land use changes to improve carbon sequestration (Smith, 2004; van Kessel *et al.*, 2006; Soussana and Luscher, 2007; Ciais *et al.*, 2010; Smith *et al.*, 2010*a*) (but see Lal, 2010*a*). However, this seems to be based in part on the present use of comparatively shallow-rooted plants that in some regions may indeed have approached the possible saturation of carbon sequestration. A particular issue is that most studies do not make soil measurements much below a metre (Nepstad *et al.*, 1994; Batjes, 1996; Canadell *et al.*, 1996; Jobbágy and Jackson, 2000; Guo and Gifford, 2002; Schenk and Jackson, 2002*a*; Robinson, 2004; Bradley *et al.*, 2005; Lorenz and Lal, 2005; Mokany *et al.*, 2006; Ichii *et al.*, 2009; Qin and Huang, 2010; Wang *et al.*, 2010), and the kinds of root depths we are looking at here would more than double that. This doubling of root biomass from a nominal 1 m to a nominal 2 m is really the key issue, together with the longevity of the roots and carbon they secrete and sequester below-ground (a complete turnover annually, including of stover in no-till systems, obviously gives no net steady-state sequestration).

The turnover rate or time is an especially important measure here. However, data on the longevity of soil roots and the (other) pools of carbon that are obtained therefrom in the soil (Zimmermann *et al.*, 2007; Smith *et al.*, 2010*b*) (let alone their variation with depth, soil type, vegetation type, etc.) are both uncertain and not very easy to come by (Baggs, 2006; Gregory, 2006; Kuz'yakov, 2006; Koerber *et al.*, 2010; Sanderman and Baldock, 2010), but Gill and Jackson (2000) indicate a loss of 40 % per year in temperate grasslands (i.e. a 'linear' lifetime of 2.5 years), with a greater decay as temperature increases, while Högberg and Read (2006) summarize some of the evidence for the increasing recognition that roots in soil are more long-lived than previously credited (see also Collins *et al.*, 2010), and there is increasing evidence for the role of physical protection (occlusion/aggregation) in improving carbon retention (e.g. Krull *et al.*, 2003; von Lützow *et al.*, 2006; Jastrow *et al.*, 2007; McCarthy *et al.*, 2008; Virto *et al.*, 2008, 2010; Moni *et al.*, 2010). The residence time of more refractory forms of SOC, albeit derived originally from manure or photosynthate, may be considerably longer (Bull *et al.*, 2000; Paustian *et al.*, 2000), and isotopic methods (e.g. Dungait *et al.*, 2008, 2009,

2010; Rubino *et al.*, 2010; Smith *et al.*, 2010*b*) have an important role to play in the analysis of the turnover of carbon-containing soil components and their biomarkers. Biochars (e.g. Lehmann, 2007; Atkinson *et al.*, 2010; Sohi *et al.*, 2010) are seen as especially recalcitrant. Clearly the rate of degradation is controlled by at least two classes of factor, the rate of biochemical alteration and the extent of physico-chemical protection (Jastrow *et al.*, 2007), and these vary among different substances. The rate of biochemical alteration of a molecule (related to its recalcitrance), and the eventual loss of carbon as CO₂, also depends on what enzymes and organisms are present that are able to degrade it under the relevant conditions (e.g. of pH, oxygen tension, etc.) (Jastrow *et al.*, 2007). Without going into the specific chemical details, there are obvious relationships between all of these and the overall ability to sequester carbon in various forms. How to ensure that deep root carbon is more recalcitrant when we know which molecules are the most recalcitrant, or have other properties desirable for building soil structure, is another goal of the breeding process.

HOW MUCH CARBON MAY BE SEQUESTERED IN THIS WAY?

It would be desirable to give a precise, quantitative answer to this question, but it is affected by so many variables that the possible range is quite large; these variables include the baseline carbon content, photosynthetic yields, microbial and other respiratory activity, root turnover, soil biophysics and aridity, soil aggregate water stability and repellency, and so on, and so we suffice with an approximation. (No attempt is made to discriminate the many known pools of soil carbon.) The key issues are the amount that can be sequestered (whether as roots or as other forms of SOC) per year, and the lifetime of the carbon so sequestered before it is eventually re-respired to the atmosphere. Most of the estimates for the carbon sequestration potential range from about 0.3 to 0.8 tC ha⁻¹ year⁻¹ (Smith, 2004), but some estimates are well outside (especially above) this range. The point, though, is that what matters is not so much what is happening now as what might be achieved with suitable breeding of plants with deep (and reasonably long-lived) roots. Increasing root mass by an extra 1 m depth with a very modest carbon content of just 1 % carbon by volume of overall soil mass equates (assuming a relative density of 1) to 10 kg m⁻² (100 t ha⁻¹), or on average 5 kg m⁻² (50 t ha⁻¹) if it turns over every 2 years. Lal (2004) indicates that some cultivated soils have lost one-half to two-thirds of their original SOC pool, with a cumulative loss of 30–40 Mg C ha⁻¹ (i.e. 30–40 t ha⁻¹), implying that these levels are a minimum that can be sequestered (since they once were), so the 50 t ha⁻¹ number seems both conservative and reasonable. Some analyses of existing grasslands and energy crops imply that at least 100 t ha⁻¹ of steady-state carbon sequestration in roots is routinely attainable (Dondini *et al.*, 2009*a*; Silver *et al.*, 2010) [forests typically sequester even more (Malhi *et al.*, 1999)], with gross global primary production exceeding 100 Pg year⁻¹ (Beer *et al.*, 2010).

The carbon being produced from fossil fuel burning is some 8.4 Gt year⁻¹ (MacKay, 2008), and so to mop this up at the rate of 50 t ha⁻¹ some 1.6 × 10⁸ ha or 1.6 × 10⁶ km² would

be required. This compares with some $41.4 \times 10^6 \text{ km}^2$ (Bot *et al.*, 2000) of just rainfed arable land, and $130.56 \times 10^6 \text{ km}^2$ of total land area excluding polar regions (<http://www.worldmapper.org/>). Thus, one thing is clear: doubling the steady-state depth of roots from approx. 1 m to 2 m can have a significantly beneficial impact on lowering the levels of atmospheric CO_2 . Since the calculations at this level of granularity are straightforward (without spatial analysis or details of economics, infrastructure issues, transitional arrangements, the time required to breed the appropriate crops and to bulk them up and to disseminate the necessary germplasm, and so on), we have made them available at <http://dbkgroup.org/carbonsequestration/rootsystem.html>. Default values include the facts that there are 2300 Mha of cropland and a similar amount of grassland (rangeland) [and note the comparatively recent loss of an additional approx. 20 % of agricultural land (Campbell *et al.*, 2008; Somerville *et al.*, 2010)], the carbon in the atmosphere (essentially as CO_2) is some 750–821 Pg (approx. 385 ppm by volume) while that in the soil is approx. 1500 Pg, and that the relative density of soil is that of water, i.e. 1. Calculations based on this imply that an extra 2 % of carbon occupying an extra 1 m depth over these areas = $20 \text{ kg m}^{-2} = 200 \text{ t ha}^{-1}$ (or, simplistically ignoring any feedbacks, 100 t ha^{-1} fixed on average in the steady state if the lifetime of the average ‘carbon’ held in different molecules is 2 years).

POSSIBLE COMPLEXITIES

This short overview has concentrated on breeding plants with deep (and bushy) roots *per se*, but I recognize that it is necessary to take a full systems approach. For instance, I have not discussed in any detail the interactions of roots with soil micro-organisms and other invertebrates. In addition, one would wish to check details of the consequences of the biochemical turnover of the deeper roots of plants (especially if waterlogged and anaerobic), lest they produce methane or nitrous oxide (Philippot *et al.*, 2009), GHGs far more potent than CO_2 (Soussana *et al.*, 2007). Other aspects of plant breeding for carbon sequestration may interact positively or negatively with, or may be decoupled from, agricultural outputs such as useful (i.e. agriculturally productive) yield. Thus an improved opening of stomata, that might assist CO_2 uptake, may also lead to greater transpirational losses. The economics of agriculture-based carbon sequestration will also be affected significantly by any carbon credits that may be applied (Smith *et al.*, 2008; MacLeod *et al.*, 2010; Smith and Olesen, 2010; Lal, 2011).

CONCLUDING REMARKS

In this brief commentary, I have sought to draw attention to the potentially substantial benefits that are to be had from breeding and growing crops with very extensive root systems. The analysis differs explicitly from the more common analysis of what pertains now as it seeks to understand what might be done by explicit human breeding of the necessary crops. In addition to the simple carbon sequestration that these imply – possibly double that of common annual grain crops – such crops seem to mobilize and retain nutrients

and water very effectively over extended periods, thus providing resistance to drought (e.g. Burch and Johns, 1978; Passioura, 1983, 2006; Ekanayake *et al.*, 1985; Champoux *et al.*, 1995; Price *et al.*, 2002a; Kato *et al.*, 2006; Kirkegaard *et al.*, 2007; Bernier *et al.*, 2008; Kamoshita *et al.*, 2008; Karcher *et al.*, 2008; Cairns *et al.*, 2009; Hund *et al.*, 2009; McKenzie *et al.*, 2009), flooding and other consequences of climate change, as well as to fertilizer runoff. In addition, the development of plants with deep roots may in fact stimulate photosynthetic yields as these are considered to be more controlled by the carbon sinks of plants (e.g. Zhu *et al.*, 2010) [demand typically being considerably more controlling than supply when one is seeking to increase biotechnological fluxes (Cornish-Bowden *et al.*, 1995; Hofmeyr and Cornish-Bowden, 2000)]. The production (by breeding) of deep roots in some cultivars will undoubtedly be at the expense of above-ground biomass yields, but there is no evidence that it has to be so (e.g. Fisher *et al.*, 1994). Thus, the research agenda is clear: we need to learn much more about those genes that control root development as part of whole plant development, the interactions of various roots with soil and soil organisms, and the actual benefits of net carbon, nutrient and water sequestration that can be effected by such crops under various agronomic conditions. This is likely to include the requirement to develop novel instrumentation (and algorithms) to measure root and other phenotypes (e.g. Nadezhdina and Čermák, 2003; Granier *et al.*, 2006; French *et al.*, 2009; Gregory *et al.*, 2009; Iyer-Pascuzzi *et al.*, 2010; Wielopolski *et al.*, 2010), as well as the informatics necessary (e.g. Jenkins *et al.*, 2004) for storing and making available such data, including the anticipated flood of genomics data. While there is a way to go before such crops might have, for example, the grain yields of present day cereals, their breeding and deployment seems a very promising avenue for sustainable agriculture.

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