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Ramesh Laungani

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The impact of co-occurring tree and grassland species on carbon sequestration and potential biofuel production

RAMESH LAUNGANI and JOHANNES M. H. KNOPS

School of Biological Sciences, University of Nebraska, 348 Manter Hall, Lincoln, NE 68588, USA

Abstract

We evaluated how three co-occurring tree and four grassland species influence potentially harvestable biofuel stocks and above- and belowground carbon pools. After 5 years, the tree *Pinus strobus* had 6.5 times the amount of aboveground harvestable biomass as another tree *Quercus ellipsoidalis* and 10 times that of the grassland species. *P. strobus* accrued the largest total plant carbon pool (1375 g C m^{-2} or $394 \text{ g C m}^{-2} \text{ yr}$), while *Schizachyrium scoparium* accrued the largest total plant carbon pool among the grassland species (421 g C m^{-2} or $137 \text{ g C m}^{-2} \text{ yr}$). *Quercus ellipsoidalis* accrued 850 g C m^{-2} , *Q. macrocarpa* 370 g C m^{-2} , *Poa pratensis* 390 g C m^{-2} , *Solidago canadensis* 132 g C m^{-2} , and *Lespedeza capitata* 283 g C m^{-2} . Only *P. strobus* and *Q. ellipsoidalis* significantly sequestered carbon during the experiment. Species differed in total ecosystem carbon accumulation from -21.3 to $+169.8 \text{ g C m}^{-2} \text{ yr}$ compared with the original soil carbon pool. Plant carbon gains with *P. strobus* were paralleled by a decrease of 16% in soil carbon and a nonsignificant decline of 9% for *Q. ellipsoidalis*. However, carbon allocation differed among species, with *P. strobus* allocating most aboveground in a disturbance prone aboveground pool, whereas *Q. ellipsoidalis*, allocated most carbon in less disturbance sensitive belowground biomass. These differences have strong implications for terrestrial carbon sequestration and potential biofuel production. For *P. strobus*, aboveground plant carbon harvest for biofuel would result in no net carbon sequestration as declines in soil carbon offset plant carbon gains. Conversely the harvest of *Q. ellipsoidalis* aboveground biomass would result in net sequestration of carbon belowground due to its high allocation belowground, but would yield lower amounts of aboveground biomass. Our results demonstrate that plant species can differentially impact ecosystem carbon pools and the distribution of carbon above and belowground.

Keywords: forest, grasslands, soil carbon

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Introduction

One of the most pronounced global anthropogenic changes is the rise in atmospheric CO_2 concentrations from the burning of nonrenewable fossil fuels (IPCC, 2007). This increase may significantly alter ecosystem carbon pools and fluxes (Zak *et al.*, 1990; Perruchoud & Fischlin, 1995) and has led to an emphasis on understanding ecosystem carbon budgets (Makela *et al.*, 2008), the development of carbon sequestration strategies (Guo & Gifford, 2002; Lal, 2008), and, more recently, research into renewable carbon negative or

carbon-neutral biofuels (Tilman *et al.*, 2006; Han *et al.*, 2007; Richter *et al.*, 2009).

In terrestrial ecosystems carbon is present in two main pools: soil organic matter (SOM) and within living and dead plants. Globally, the SOM pool is a much larger pool than the plant carbon pool (Batjes, 1996; Schlesinger, 1997; Amundson, 2001), with the SOM carbon pool having a much slower turnover rate than the plant carbon pool (Schlesinger, 1997; Knops *et al.*, 2002). This provides the potential for storing large amounts of carbon in the SOM pool; however the rate of change and the annual accumulation in the SOM can be small and slow (Schlesinger, 1997; Knops *et al.*, 2002). Despite its large size and recalcitrance, the SOM pool can vary by one to two orders of magnitude among ecosystems (Post *et al.*, 1982, 1985). For example, the

Correspondence: Ramesh Laungani, tel. +402 250 7873, e-mail: ramesh_laungani@yahoo.com

SOM pool in temperate grasslands has been found to be almost three times larger than temperate forests (Post *et al.*, 1982, 1985; Johnston *et al.*, 1996; Knops & Bradley, 2009). In addition there can be large differences in the size of the SOM carbon pool associated with different plant species in both managed and natural systems. Lemma *et al.* (2006) found 69.6 and 29.3 Mg C ha⁻¹ in the soil after 20 years in plantations of *Cupressus lusitanica* and *Pinus patula* stands, respectively. In a natural grassland system Mahaney *et al.* (2008) found a 30–40% difference in SOM levels between plots dominated by different coexisting perennial grass species. These ecosystem and species differences in SOM carbon pool size illustrate that changes in species composition, either natural or human induced, can lead significant long-term changes in the carbon that is stored in SOM (Jackson *et al.*, 2002). However, it is not clear how much the SOM carbon pool can change over shorter time periods in the early establishment phase of new species, and if certain changes in species composition will cause the SOM pool to act as a carbon source or sink in the short term (Mahaney *et al.*, 2008; Dowell *et al.*, 2009).

The other key terrestrial carbon pool is the carbon present in living and dead plant material. Plant carbon is distributed between aboveground and belowground structures, and this distribution can vary among ecosystems (Jackson *et al.*, 1996) and among species within ecosystems (Craine *et al.*, 2001, 2002; Tjoelker *et al.*, 2005). Among ecosystems the size of the plant carbon pool can vary by two orders of magnitude, ranging from 0.97 kg C m⁻² in deserts to 30.7 kg C m⁻² in tropical evergreen forests (Jackson *et al.*, 1996). In addition, Jackson *et al.* (1996) found that the ratio of belowground to aboveground plant carbon ranged from 0.18 to 3.7 between coniferous forests and temperate grasslands, respectively. Within temperate grasslands, Wedin & Tilman (1990) found that allocation of plant carbon to belowground structures ranged from 35% to 85% of total plant carbon among five perennial grass species which naturally co-occur. Thus different species and changes in species composition can result in large pools of standing plant carbon over relatively short time periods and variation among species within ecosystems can also impact the size and distribution of the plant carbon pool.

Furthermore, variation among species in the distribution of plant carbon between above and belowground plant carbon pools has consequences for the potential harvest of aboveground plant carbon for biofuels and for sequestration of atmospheric carbon into plant biomass (Sartori *et al.*, 2006). Recent studies have shown that aboveground plant carbon can be harvested as a potential source of biofuel in both grassland and forested ecosystems (Tilman *et al.*, 2006; Richter *et al.*,

2009). Alternately, since aboveground plant carbon can be lost from disturbances such as fire and windstorms, species differences in proportional allocation of aboveground and belowground plant carbon pools may significantly impact the rate of ecosystem carbon accumulation belowground in disturbance prone systems (Williams *et al.*, 2004). An understanding of these species impacts on both plant and soil carbon pools is important for implementing successful carbon sequestration strategies (Farley *et al.*, 2004). While certain highly productive species may sequester atmospheric carbon into plant biomass causing net increases in ecosystem carbon stocks, it is also important to evaluate whether large standing ecosystem carbon stocks, like those found in grassland soils (Post *et al.*, 1982), can be maintained with the establishment of less productive species which may not significantly increase total ecosystem carbon through plant carbon gains but cause little to no changes in long-term carbon storage in SOM. Therefore, as plant species composition can alter both the size and distribution of the plant carbon pool and the size of the SOM pool, both management goals require an understanding of species impacts on SOM and plant carbon pools (Farley *et al.*, 2004; Tilman *et al.*, 2006; Gough *et al.*, 2008).

If a management practice is being evaluated for potential biofuel harvest, such as the establishment of forest plantations (Smith & Scherr, 2002; Richter *et al.*, 2009) or diverse grassland plots (Tilman *et al.*, 2006), it is critical to evaluate both the allocation of plant carbon between above and belowground plant carbon pools in the species of interest as well as the impact of the species (or assemblage of species) on the SOM pool. An understanding of these species impacts will help determine how much the harvesting of aboveground plant carbon for biofuel production will reduce ecosystem carbon stocks and whether aboveground harvest will result in a larger than expected loss of ecosystem carbon through concurrent declines in soil carbon (Dowell *et al.*, 2009). The harvest and combustion of aboveground biomass for biofuel recirculates carbon between the plant and atmosphere. However, if the harvest of plant carbon for biofuel production is also accompanied by large losses of SOM this may result in a net increase in atmospheric CO₂. Plant carbon gains can be offset by losses in SOM which are equal to or greater than plant carbon gains, causing no net change or overall declines in total ecosystem carbon stocks, respectively (Jackson *et al.*, 2002).

Ideally, plant species (or sets of species) used as a source of biofuel would allocate large amounts of biomass aboveground for harvest while concurrently sequestering carbon belowground into either root biomass or causing an increase in the long-term storage of

carbon in the SOM pool (Sartori *et al.*, 2006). Recent work has shown that diverse assemblages of grassland species can be highly productive aboveground while simultaneously increasing SOM levels (Tilman *et al.*, 2006). These belowground gains in SOM can offset aboveground carbon losses from harvesting resulting in net carbon storage (Tilman *et al.*, 2006). While this strategy may seem ideal for biofuel production, biomass from grasslands must be harvested annually and therefore biomass yield is subject to annual variability in productivity which can be significant in these systems (Knapp & Smith, 2001), with up to 50% lower biomass production in dry years (Tilman & Downing, 1994). Alternatively many tree species may be better suited for biofuel production (Richter *et al.*, 2009) as they are not subject to the same annual variability in biomass production (Knapp & Smith, 2001), allocate a significant proportion of their carbon to aboveground structures, do not require annual biomass harvest, and cumulatively over longer time scales may produce more harvestable biomass than annual grassland harvests for an equivalent number of years.

To understand plant species impacts on total ecosystem carbon stocks, the distribution of ecosystem carbon between plant and soil pools, allocation of plant carbon between aboveground and belowground plant carbon pools, and potentially harvestable biofuel stocks, we evaluated seven grassland and forest species in replicate monocultures in a common garden experiment. We examined one conifer tree species, two hardwood tree species, two grass species, a legume species, and a forb species. These species were chosen because they are potentially dominant at our study site. A strength of our experimental design was that we utilized replicate monocultures which were all initially established in identical soil rather than using a series of paired sites with different species composition (Briggs *et al.*, 2002; Jackson *et al.*, 2002; McKinley & Blair, 2008) to evaluate species impacts on carbon pools. The use of replicate monocultures allowed us to attribute observed changes in ecosystem carbon pools to species differences and was not confounded by differences in original soil characteristics (i.e., original soil fertility, clay content, etc.). In addition, the nutrient poor soil used in each monoculture is ideal for simultaneously examining species impacts on the potential of species as a source of biofuels and the belowground soil carbon pool as the use of marginal lands (i.e., abandoned agricultural fields) is being advocated for biofuel production (Fargione *et al.*, 2008). Furthermore using our approach can address whether or not species driven changes in the SOM pool might offset potentially harvestable aboveground carbon. However, this design does not incorporate different starting conditions that often naturally

occur because of differences in carbon pools among different vegetation types (Post *et al.*, 1982, 1985; Johnston *et al.*, 1996). In addition, we can only address monocultures, not any possible interactions of co-occurring species and any changes occurring over longer time periods. In addition the monocultures were established with disturbed soil from the surrounding ecosystem and this might have lead to a carbon loss (Wardle, 2002). However, this disturbance should be the same for all species and by including a bare soil treatment we can evaluate species changes.

Using these replicate monocultures our study specifically focused on four questions: (1) How much aboveground biomass (i.e. potentially harvestable biofuel carbon) do different plant species accumulate annually and cumulatively over an extended time? (2) To what degree do plant species differentially influence total carbon pools and the distribution of carbon between above- and belowground pools? (3) Are species which allocate high amounts of carbon aboveground, associated with decreased plant carbon pools belowground, thereby reducing the potential to sequester carbon long term in the soil? (4) Can carbon be sequestered even with the harvest of aboveground plant carbon for biofuels?

Methods

Experimental mesocosm setup and site description

We examined species effects on total ecosystem carbon stocks by comparing three tree species, *Pinus strobus*, *Quercus ellipsoidalis*, and *Quercus macrocarpa*, and two dominant grasses; the introduced C₃ *Poa pratensis* and the native C₄ *Schizachyrium scoparium* at Cedar Creek Ecosystem Science Reserve in central Minnesota (hereafter Cedar Creek). The vegetation at Cedar Creek is made up of successional and prairie-like grasslands, oak savannas, woodlands, and wetlands. Grasslands are dominated by warm season C₄ grasses such as *S. scoparium*, *Andropogon gerardii*, and *Sorghastrum nutans*, and by introduced C₃ species such as *P. pratensis* and *Bromus inermis*, and the woodland areas are composed of mixed stands of *P. strobus* and *Quercus* spp. In addition we included two forbs that can attain high abundances locally, the nitrogen fixer *Lespedeza capitata* and the clonal *Solidago canadensis*. In this study grassland species are considered all nonwoody species. The mean annual temperature at Cedar Creek is 5.7 °C and the mean annual precipitation is 660 mm. Soils are sandy and derived from glacial outwash (Grigal *et al.*, 1974), with nitrogen being the primary resource limiting plant productivity (Tilman, 1984). At Cedar Creek there are distinct differences between the total ecosystem

carbon pools of the major community types (Johnston *et al.*, 1996) with coniferous forests storing 353 Mg ha^{-1} , deciduous forests storing 450 Mg ha^{-1} , and grasslands storing 137 Mg ha^{-1} . In grasslands the vast majority of the measured ecosystem carbon is stored in the top 25 cm of the soil carbon pool (132 Mg ha^{-1}), while coniferous forests store close to 40% of the measured carbon in the top 25 cm of the soil (139 Mg ha^{-1}) and deciduous forests store 30% of the measured carbon in the top 25 cm of the soil (133 Mg ha^{-1}) (Johnston *et al.*, 1996). Although these data show that there are nearly equivalent soil carbon stocks between grassland and forest soils, the high allocation of plant carbon belowground of grassland species can lead to large pools of carbon at deeper depths (Craine *et al.*, 2003). Recent work has shown that there can be large stores of soil carbon at deeper soil depths below the first 25 cm in grassland soils (Knops & Bradley, 2009).

Experimental mesocosms were established at Cedar Creek Ecosystem Science Reserve in central Minnesota, USA in late 2000. Mesocosms consisted of circular pots which were 60 cm in diameter and 50 cm in depth, and from which roots could not escape. Mesocosms were dug into the ground so that the top of the pot was flush with the soil surface. Each pot was filled with locally collected representative field soil, with the lower 40 cm being filled with subsurface soil and the top 10 cm being filled with topsoil. In 2006 both *S. scoparium* and *P. pratensis* had achieved over 90% coverage of the soil surface in their respective mesocosms, *L. capitata* had an average density of $110.6 \text{ individuals m}^{-2}$, *Solidago altissima* had an average density of $130 \text{ individuals m}^{-2}$, *Q. ellipsoidalis* had an average density of $82.5 \text{ individuals m}^{-2}$, *Q. macrocarpa* had an average density of $79 \text{ individuals m}^{-2}$, and *P. strobus* had average density of $49.5 \text{ individuals m}^{-2}$. We also established six replicate control mesocosms in which no vegetation was established and were maintained through periodic hand weeding. We examined species effects on total carbon pools by quantifying aboveground (stems, leaves, and litter carbon) and belowground (soil and root carbon) carbon associated with the seven plant species in the study.

Soil sampling and analysis

In order to determine species driven changes on the SOM pool, we sampled soil at three depths in early spring 2001 and early fall 2006 (0–10, 10–25, and 25–50 cm). Soil % carbon was determined using combustion analysis from a Costech analytical (Valencia, CA, USA) ECS 4010 (University of Nebraska-Lincoln, Ecosystem Analysis Laboratory). Soil % carbon was converted to g carbon m^{-2} at each sampled depth following an equation which determined soil bulk density speci-

ally for soil at Cedar Creek (Wedin & Tilman, 1990). Measured values of soil bulk density on a subset of mesocosms at 0–10 cm ($\sim 1.40 \text{ g cm}^{-3}$) and 10–25 cm ($\sim 1.48 \text{ g cm}^{-3}$) were comparable to those calculated following the equation ($\sim 1.45 \text{ g cm}^{-3}$). No bulk density measurements were taken from 25 to 50 cm. We found no significant differences in soil carbon between species in the 2001 soil sampling; therefore change in soil carbon pool of each mesocosm was the difference between the average soil carbon content from the 2001 sampling and the measured soil carbon content in 2006 from each mesocosm.

Plant sampling

Above and belowground biomass was harvested in 2006 in all experimental mesocosms. Aboveground biomass was sampled in a $10 \text{ cm} \times 60 \text{ cm}$ strip through the center of the pot and was separated into leaves, stems (for *Quercus* species, *P. strobus*, *S. altissima*, and *L. capitata*), and leaf litter. For the woody species the clipped area contained two to three individual trees, which were all harvested, this is equivalent to $33\text{--}66 \text{ individuals m}^{-2}$. Belowground biomass was sampled at three points within the clipped area at three depths (0–10, 10–25, and 25–50 cm) using a 2 in. diameter core. Each pool of plant biomass (leaves, stems, litter, roots, and root ingrowth) was dried to a constant weight and analyzed for carbon content using combustion analysis from a Costech analytical ECS 4010. Plant biomass was multiplied by measured carbon concentrations to determine plant carbon mass.

Total ecosystem carbon stocks and annual change in carbon pools

At the start of the experiment total ecosystem carbon stocks were equal to the average soil carbon pool across all mesocosms, as there were no significant differences among species in initial soil carbon pools and there was no plant biomass at the time of the initial soil sampling. In 2006, total ecosystem carbon stocks were calculated as the sum of all plant carbon pools and the soil carbon pool. Annual belowground carbon change was the sum of annual root carbon and annual soil carbon change. After five growing seasons, annual soil carbon change was calculated as $1/5$ of the difference between 2001 and 2006 soil carbon pools. Similarly, annual root carbon change was calculated as $1/5$ of standing root carbon. While this calculation assumes linear increases in root growth among species, by 2006 we assumed that belowground biomass was at steady state (Reich *et al.*, 2006) making this a safe assumption for the calculation of annual root growth. Other work conducted at the

same site showed that after 3–4 years biomass yields were also at steady state and sampling of both above and belowground biomass was carried out after 5 years (Reich *et al.*, 2006). For all nonwoody species annual aboveground carbon change was determined as the sum of standing leaf carbon and standing stem carbon (for *S. altissima* and *L. capitata*). For the two oak species, annual aboveground carbon gain was the sum of standing leaf carbon, and 1/5 of stem carbon. For *P. strobus*, annual carbon gain was the sum of 1/2 standing leaf carbon, and 1/5 of stem carbon. Only 1/2 of standing leaf carbon was used for *P. strobus* because leaf longevity was estimated at 2 years.

Statistical analysis

Data was analyzed in SPSS v. 17 (SPSS Statistics, SPSS Inc., Chicago, 2008). As all mesocosms were initially established on identical soils and we utilized the same average 2001 soil carbon across all the pots as the initial starting value for total mesocosm carbon, we analyzed the 2006 total mesocosm carbon to see if it differed from the 2001 soil carbon average using one-way analysis of variance (ANOVA) with year as a fixed factor for each species. Species differences in plant and soil response variables were examined using one-way ANOVA with species as a fixed factor. Differences between individual species were examined using *post hoc* Tukey's tests ($P < 0.05$).

Results

We found that species differed markedly in total aboveground biomass that could be harvested for biofuel production. For all species, all living aboveground biomass was considered harvestable (Tilman *et al.*, 2006). Annually, *P. strobus* produced significantly more harvestable biomass than the other species in the study (Table 1). Over 5 years this resulted in *P. strobus* producing more than 6.5 times the amount of harvestable biomass as *Q. ellipsoidalis*, the next most productive species in the study. In addition for *P. strobus*, harvestable biomass for biofuel was more than 12 times higher than *S. scoparium* and nearly 20 times higher than *P. pratensis* after 5 years. This translated in *P. strobus* being 2.8 and 4.5 times greater annually as compared with *S. scoparium* and *P. pratensis*, respectively. This is significant as these dominant grasses have been considered as sources of harvestable biofuel (Tilman *et al.*, 2006). Even when only the woody stem carbon from trees is considered for biofuel harvest, *P. strobus* produced more than seven times more harvestable stem biomass than the living aboveground carbon of *S. scoparium* and nearly 14 times more than *P. pratensis* over 5 years.

Among the tree species *P. strobus* produced more than nine times as much harvestable woody carbon as *Q. ellipsoidalis* and more than 15 times as much woody carbon than *Q. macrocarpa* (Table 1).

Over a 5-year period, species differed in total ecosystem carbon accumulation from -4% to 26% as compared with the original pool of soil carbon. However, only *P. strobus* and *Q. ellipsoidalis* accumulated a significant amount of carbon during the experiment (Fig. 1). Over 5 years, *P. strobus* and *Q. ellipsoidalis* increased total carbon stocks by 26% or 169 g C m⁻² yr and 17% or 110 g C m⁻² yr, respectively. The bare soil mesocosms showed a marginally significant ($P = 0.051$) 13% decline of total ecosystem carbon (Fig. 1) equivalent to a loss of 87 g C m⁻² yr. We found that most plant species (five of seven) did not cause significant changes in total ecosystem carbon stocks over the 5-year period, although there was a large range of changes among species, and only two of the three woody species increased total ecosystem carbon stocks.

During the experiment *P. strobus* and *S. scoparium* had significant declines in soil carbon, similar to the bare soil control, with each species losing 16% of the original soil carbon equivalent to 526 g C m⁻² (Table 1) or 105 g C m⁻² yr. The other species showed no significant change in the total soil carbon pool, although there was a nonsignificant increase in soil carbon beneath *S. canadensis* of 220 g C m⁻² (Table 1). The changes in soil carbon under *P. strobus* and *S. scoparium* were driven by significant loss in the top 25 cm of the soil profile. *P. strobus* had a loss of 35% of soil carbon from the top 10 cm and a loss of 19% from 10 to 25 cm (Table 1). *S. scoparium* had a loss of 15% and 20% from depths 0 to 10 and 10 to 25 cm, respectively (Table 1). Other species which did not show significant changes in total soil carbon did however significantly change different parts of the soil profile (Table 1). For example, the SOM pool beneath *Q. ellipsoidalis* showed a nonsignificant loss of 16 g C m⁻² in the top 10 cm but a significant loss of 124 g C m⁻² from 10 to 25 cm. Conversely, there was a significant loss of 98 g C m⁻² in the top 10 cm underneath *Q. macrocarpa*, but no significant change in the lower soil depths (Table 1).

Among species plant carbon pools differed significantly in both size and distribution between above and belowground. We found that *P. strobus* accrued the largest pool of plant carbon over 5 years, 1375 g C m⁻², which was more than 1.5 times higher than the next most productive species *Q. ellipsoidalis* (Table 1; 850 g C m⁻²) and more than three times as high relative to all other species (Table 1). For the tree species, *Q. macrocarpa* had the lowest total plant carbon accrual after 5 years (Table 1; 370 g C m⁻²). Surprisingly this low level of productivity was comparable to the grassland species

in the study, which averaged 306 g C m^{-2} . Among the grassland species, *S. scoparium* accrued the largest total plant carbon pool (Table 1; 421 g C m^{-2}), and *P. pratensis* had the next largest pool of plant carbon (Table 1; 391 g C m^{-2}). *S. canadensis* had the lowest plant carbon accrual among the species in the study (Table 1; 132 g C m^{-2}). From our estimation of annual carbon gain (see Methods), we also found that *P. strobus* had significantly larger annual plant carbon gain than all other species in the study (Table 1; $394 \text{ g C m}^{-2} \text{ yr}$). Among the grassland species *S. scoparium* had the largest annual plant carbon gain (Table 1; $137 \text{ g C m}^{-2} \text{ yr}$). This was more than 1.5 times as large as *P. pratensis* and more than twice as large as the lowest grassland species *S. canadensis* (Table 1; $62 \text{ g C m}^{-2} \text{ yr}$). In addition, we found significant differences among species in plant carbon allocation between aboveground (leaves and stems) and belowground structures (roots). Allocation of plant carbon to aboveground structures across species ranged from 19% to 75%. *P. strobus* allocated significantly more carbon into aboveground structures than all other species, while *Q. ellipsoidalis* allocated over 80% of its carbon into roots (Table 1). All the grassland species allocated the majority of their plant carbon into roots. *S. scoparium* and *L. capitata* both proportionally allocated the most belowground among the grassland species (67%). In addition, there was more than a three-fold difference in the annual rate aboveground carbon accumulation between *P. strobus* and all other species (Fig. 2). The two oak species did not differ in their annual aboveground biomass accumulation from *S. scoparium* and *L. capitata*.

Discussion

Species impacts on potential biofuel stocks

Our study demonstrates that woody species with high productivity and high allocation of plant carbon aboveground, such as *P. strobus*, may be good candidates for potential biofuel harvest. After 5 years, the tree *P. strobus* had the greatest potential for biofuel production with 6.5 times the amount of aboveground harvestable biomass as another tree *Q. ellipsoidalis* and 10 times that of the grassland species. Recent work has suggested that diverse assemblages of grassland species can be used as a source of renewable carbon-negative biofuel (Tilman *et al.*, 2006), however our results demonstrate that woody species such as *P. strobus* may provide significantly more carbon aboveground that can be harvested for biofuel production as compared with grassland species (Table 1). One drawback to the use of grassland species as a potential source of biofuel is that harvest of aboveground carbon is required an-

nually at the risk of losing that biomass to senescence even when yields are not at a maximum due to annual variability in grassland species productivity (Tilman & Downing, 1994; Knapp & Smith, 2001). However, woody species such as *P. strobus* do not need annual harvest and are not susceptible to the same annual variability in productivity (Knapp & Smith, 2001) which may provide a more consistent yield of aboveground plant carbon as compared with grassland species if harvested on a half-decadal or decadal time scale. The use of wood as a source of renewable biofuel has already been implemented in a number of countries in Europe (Richter *et al.*, 2009), and the capability of American foresters to produce over 350 million dry tons of wood biomass (Richter *et al.*, 2009) also supports the use of species like *P. strobus* for potential biofuel harvest. Furthermore, our experimental mesocosms were established in nutrient poor soil making species such as *P. strobus* ideal for maximizing aboveground plant carbon harvest in systems such as agriculturally degraded land which have marginal soil quality (Tilman *et al.*, 2006).

However the use of woody species for biofuel production is not without its drawbacks as well. Although woody species such as *P. strobus* may not require annual harvest like grassland species and can produce large amounts of potentially harvestable biofuel, the significant decline in soil carbon associated with *P. strobus* highlights the need to understand both above and belowground changes associated with the establishment of woody species for biofuel production. Combustion of aboveground plant carbon for biofuel, if accompanied with large losses of soil carbon, may result in a net flux of CO_2 to the atmosphere. Our results indicate that woody species which produce large amounts of aboveground biomass which can be harvested for biofuel may come at the cost of ecosystem carbon increases from belowground plant carbon (e.g. *P. strobus*). Conversely increases in ecosystem carbon from belowground plant carbon gains may reduce the yield of aboveground carbon that can be harvested for biofuel (e.g. *Q. ellipsoidalis*).

Species impacts on the size and distribution of ecosystem carbon pools and carbon sequestration

The high productivity of *P. strobus* and resulting net increase in total ecosystem carbon stocks may support the use of pines in carbon sequestration strategies (Smith & Scherr, 2002). However the significant gain in total ecosystem carbon was driven by the large pool of aboveground plant carbon and also was accompanied by a large decline in soil carbon. The large pool of aboveground plant carbon in *P. strobus* makes the system susceptible to large losses of plant carbon

Table 1 Changes in soil, plant, and total carbon pools among species

g C m ⁻²	<i>Pinus strobus</i>	<i>Quercus ellipsoidalis</i>	<i>Quercus macrocarpa</i>	<i>Poa pratensis</i>	<i>Schizachyrium scoparium</i>	<i>Solidago canadensis</i>	<i>Lespedeza capitata</i>	Bare soil	F; P
ΔSoil C									
Depth									
0–10 cm	-302.51* (62.42) ^b	-16.54 (52.53) ^a	-98.39* (39.36) ^{ab}	-64.30 (59.35) ^a	-130.37* (36.84) ^{ab}	21.19 (52.45) ^b	-48.56 (63.99) ^a	-36.69 (31.82) ^a	F _{7,43} = 3.98; 0.003
10–25 cm	-226.22* (68.60)	-124.83* (49.49)	-28.24 (82.11)	-21.81 (132.97)	-244.63* (96.37)	-40.14 (157.79)	-94.09 (118.65)	-200.14 (103.92)	F _{7,43} = 0.850; 0.544
25–50 cm	2.36 (85.11)	-158.35 (96.53)	27.09 (126.65)	-12.58 (59.85)	-151.91 (71.20)	239.43 (188.74)	-48.44 (175.99)	-197.50 (97.93)	F _{7,43} = 1.46; 0.213
Total	-526.36* (182.29)	-299.73 (159.61)	-99.54 (163.93)	-98.70 (196.61)	-526.92* (149.34)	220.48 (383.01)	-191.10 (238.39)	-434.34 [†] (210.10)	F _{7,43} = 1.44; 0.214
ΔPlant C									
Aboveground	1037.69 (61.55) ^c	156.84 (34.95) ^b	121.71 (19.26) ^b	168.20 (25.46) ^b	138.55 (15.26) ^b	47.61 (9.33) ^a	87.90 (6.52) ^{ab}	N/A	F _{6,37} = 115.64; 0.000
Stems	612.95 (30.79) ^c	67.49 (18.11) ^b	40.50 (8.18) ^{ab}	N/A	N/A	17.28 (3.31) ^b	41.73 (3.38) ^a	N/A	F _{4,25} = 54.02; 0.000
Leaves	407.71 (35.18) ^d	89.29 (17.03) ^c	80.76 (12.85) ^{bc}	44.24 (3.97) ^{ab}	80.75 (11.28) ^b	28.16 (5.54) ^a	41.70 (6.10) ^{ab}	N/A	F _{6,37} = 60.06; 0.000
Litter	17.02 (5.80) ^d	0.064 (0.0646) ^c	0.442 (0.4423) ^{bc}	123.95 (22.32) ^{ab}	57.80 (5.80) ^{bc}	2.17 (1.09) ^a	4.45 (2.57) ^{ab}	N/A	F _{6,37} = 22.62; 0.000
Roots	337.68 (41.09) ^a	693.36 (100.23) ^b	248.56 (106.00) ^a	222.77 (17.20) ^a	282.02 (20.33) ^a	84.31 (19.98) ^a	195.19 (26.95) ^a	N/A	F _{6,37} = 8.67; 0.000
Total	1375.37 (73.47) ^c	850.21 (104.89) ^b	370.27 (104.04) ^a	390.98 (31.92) ^a	420.58 (28.96) ^a	131.93 (24.46) ^a	283.09 (22.99) ^a	N/A	F _{6,37} = 35.10; 0.000
Aboveground proportional allocation	75.5 (0.026) ^c	18.8 (0.039) ^a	41.7 (0.071) ^b	42.1 (0.040) ^b	32.8 (0.023) ^{ab}	38.7 (0.073) ^{ab}	32.1 (0.048) ^{ab}	N/A	F _{6,36} = 14.89; 0.000

Belowground proportional allocation	24.5 (0.026) ^a	81.2 (0.039) ^c	58.2 (0.071) ^b	57.8 (0.040) ^b	67.1 (0.023) ^{ab}	61.3 (0.073) ^{ab}	67.9 (0.048) ^{ab}	N/A	$F_{6,36} = 14.89$; 0.000
Annual aboveground carbon (g C m ⁻² yr)	326.44 (22.60) ^c	102.79 (20.59) ^b	88.86 (13.98) ^b	44.24 (3.97) ^a	80.75 (11.28) ^{ab}	45.44 (8.70) ^a	83.44 (5.37) ^b	N/A	$F_{6,37} = 43.68$; 0.000
Annual root carbon (g C m ⁻² yr)	67.53 (8.21) ^b	138.67 (20.04) ^a	49.71 (21.20) ^b	44.55 (3.44) ^b	56.40 (4.06) ^b	16.86 (3.99) ^b	39.03 (5.39) ^b	N/A	$F_{6,37} = 8.67$; 0.000
Annual plant carbon (g C m ⁻² yr)	393.98 (23.59) ^d	241.46 (27.93) ^c	138.58 (20.31) ^b	88.80 (6.15) ^{ab}	137.16 (12.18) ^b	62.30 (10.59) ^a	122.48 (5.65) ^b	N/A	$F_{6,37} = 37.75$; 0.000
Δ ME/SCSM									
Total (soil + plant)	849.00 (210.61) ^{b*}	550.48 (160.21) ^{b*}	270.72 (162.46) ^{ab}	292.27 (220.61) ^{ab}	-106.34 (160.44) ^{ab}	352.41 (374.92) ^{ab}	91.98 (227.36) ^{ab}	-434.34 (210.10) ^a	$F_{7,43} = 3.77$; 0.004

All values in g C m⁻² except annual plant carbon changes. Species differences for a given response variable were examined using one-way ANOVA (F-statistics and significance in last column). Letters represent significant differences across species from *post hoc* Tukey's tests ($P < 0.05$). Values in parentheses are standard errors for a given mean. Changes in soil carbon were calculated by subtracting soil carbon in 2006 from average 2001 soil carbon by depth. Average 2001 soil carbon pool 0–10 cm: 845.90; average 2001 soil carbon pool 10–25 cm: 1201.99; average 2001 soil carbon pool 25–50 cm: 1190.16.

*Represent change in soil pool that is significantly different from 0. For *P. strobus* and *Quercus* species 'stems' is aboveground woody carbon and for *L. capitata* and *S. canadensis* 'stems' is nonleaf aboveground carbon. N/A stands for 'not applicable' as bare soil plots did not have an associated plant carbon measurements.

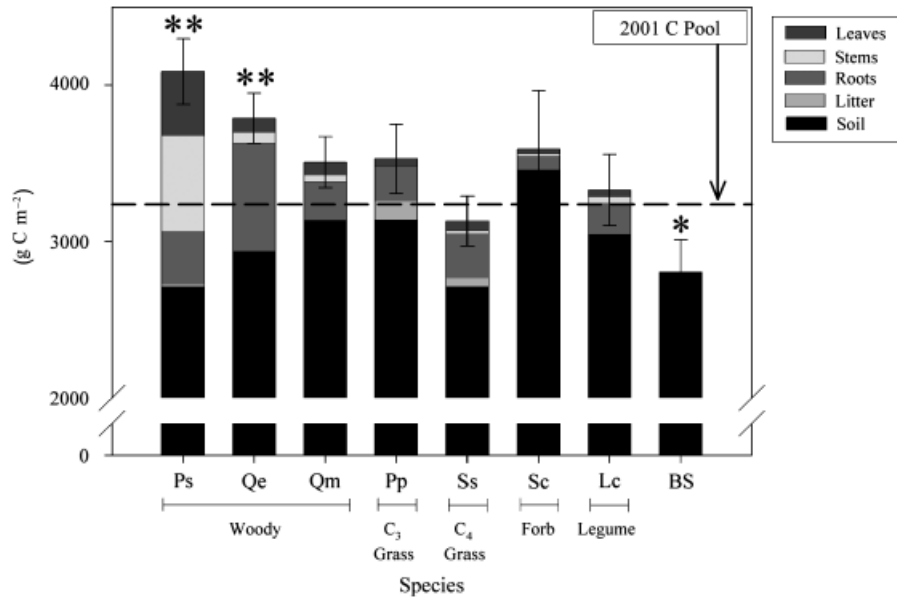


Fig. 1 Species impacts on total ecosystem carbon stocks. The dotted line represents an average of 2001 soil carbon pool among all species. No differences were found among species in 2001 soil carbon. Species changes in ecosystem carbon stocks were examined using one way ANOVA and asterisks represent significant differences from 2001 soil carbon pool (* $P < 0.1$; ** $P < 0.05$). Ps, *Pinus strobus*; Qe, *Quercus ellipsoidalis*; Qm, *Q. macrocarpa*; Lc, *Lespedeza capitata*; Pp, *Poa pratensis*; Ss, *Schizachyrium scoparium*; Sc, *Solidago canadensis*; BS, bare soil. Error bars represent ± 1 SE on total mesocosm carbon (plant + soil).

through catastrophic disturbance (Williams *et al.*, 2004). The associated decline in SOM significantly reduced the magnitude of the gain in ecosystem carbon for *P. strobus*. This is exemplified in our study by the decline in SOM over five growing seasons (526 g C m^{-2}) associated with *P. strobus* which was nearly 40% of the plant carbon pool. Both plant carbon allocation patterns and associated changes in soil carbon must be taken into consideration (Farley *et al.*, 2004) in order to ensure that plant carbon gains are not lost through disturbance or offset by loss of SOM. If declines in SOM are generally associated with pine species (Farley *et al.*, 2004), then these changes in SOM associated with the establishment of pine species could have significant consequences for total ecosystem carbon stocks and terrestrial carbon sequestration in a number of ecosystems given the high number of invasive pine species (Grotkopp *et al.*, 2002) and their use in plantations (Smith & Scherr, 2002; Farley *et al.*, 2004) globally. The observed decline in soil carbon with *P. strobus* in our study may be driven by two factors: 1) high tissue longevity of aboveground plant carbon in *P. strobus* and 2) equivalent rates of microbial SOM decomposition among species (Laungani & Knops, 2009). Given equal plant carbon pools among species, the woody stems and evergreen needles of *P. strobus* increases aboveground tissue longevity and in turn reduces the flux of plant carbon back to the soil as compared with the other species in the study.

Equivalent rates of microbial SOM decomposition among species would result in an equivalent loss of carbon from the soil pool through microbial respiration. Therefore, as compared with the other species in the study, the combination of equivalent carbon losses from the soil via microbial respiration and a reduced flux of plant carbon back to the soil (i.e. litterfall) would result in retention of carbon in the plant pool and subsequently a net decline in soil carbon associated with *P. strobus* as the SOM that is microbially broken down is annually replenished very slowly underneath *P. strobus*.

Alternately, *Q. ellipsoidalis*, which also caused net sequestration of ecosystem carbon, may be a more suitable candidate in carbon sequestration strategy as the increase in total ecosystem carbon stocks was driven by gains in belowground plant carbon and there was no significant decline in total soil carbon stocks (Table 1). This result is highlighted by the fact that in our study the sum of the SOM and belowground plant carbon pools associated with *Q. ellipsoidalis* was significantly larger than the original soil carbon pool at the start of the experiment (Fig. 1). At steady state, the higher carbon allocation belowground and higher annual root growth of *Q. ellipsoidalis* compared with *P. strobus* (Table 1), may lead to faster replenishment of the SOM pool as hardwood tree species have been shown to have higher rates of root turnover as compared with conifer species

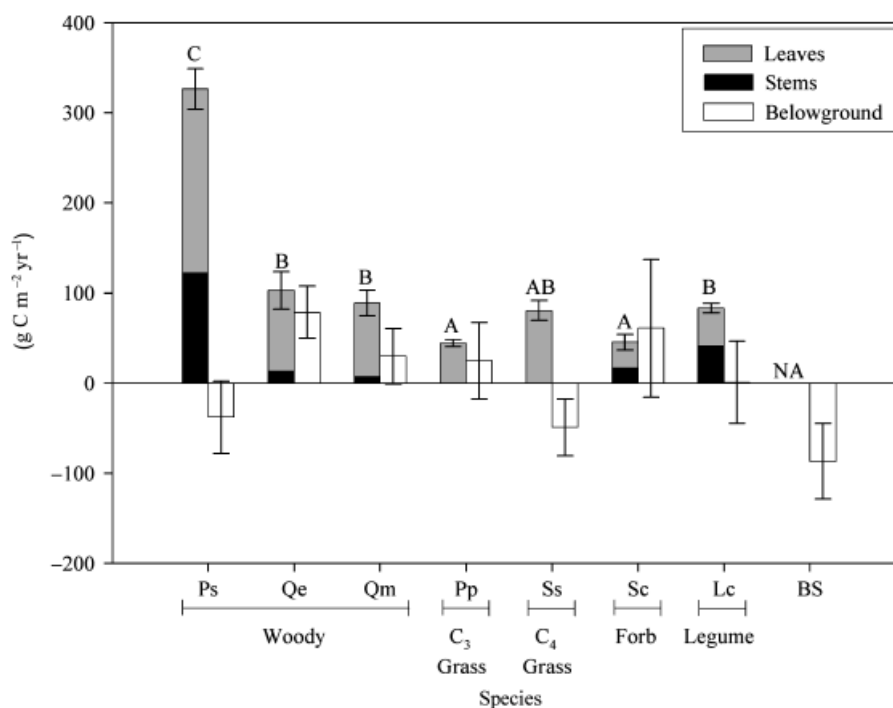


Fig. 2 Species differences in annual rate of above- and belowground carbon change. Aboveground change is the sum of annual change in leaf carbon and stem carbon. Belowground change is the sum of annual root carbon and annual soil carbon change. Letters represent significant differences across species for total aboveground annual carbon change and belowground carbon change from *post hoc* Tukey tests ($P < 0.05$). Black bars represent annual rate of change in stem carbon, gray bars represent annual rate of change in leaf carbon, and white bars represent annual rate of change in belowground carbon. Error bars represent ± 1 SE on total annual rate of change. N/A stands for 'not applicable' as bare soil plots did not have an associated annual rate of aboveground change. For species abbreviations see Fig. 1.

(Matamala *et al.*, 2003; Guo *et al.*, 2007). Taken together these results not only suggest that those species which allocate less biomass aboveground alternately allocate more biomass belowground, but also illustrate that while the establishment of woody species may increase ecosystem carbon sequestration that it may be more beneficial to plant woody species which allocate more plant carbon belowground such as *Q. ellipsoidalis* in order to sequester carbon in long-term carbon pools belowground. Similarly, *S. scoparium* was able to offset significant declines in soil carbon with large gains in belowground plant carbon making *S. scoparium* carbon-neutral. The other grassland species were also carbon-neutral, offsetting smaller losses of soil carbon with gains in plant carbon. Although it was a nonsignificant increase in total ecosystem carbon, *S. canadensis* did show substantial increase in soil carbon over 5 years, and this may point to certain grassland species actually being able to increase ecosystem carbon stocks faster than others making them more suitable candidates for use in a carbon sequestration strategy (Tilman *et al.*, 2006). Overall these results demonstrate that variation in plant carbon allocation among species can differen-

tially impact the potential for species to sequester carbon, and that declines in SOM can be offset both by above and belowground plant carbon gains, particularly with woody tree species.

However even within woody species, which allocate high amounts of plant carbon belowground, the lack of net carbon sequestration observed with *Q. macrocarpa* highlights the idiosyncratic effects that species can have on total ecosystem carbon stocks. This result may be explained by the growth strategy of *Q. macrocarpa* as it is very fire resistant and grows slowly (Johnson, 1990). While it does display rapid root development and high biomass allocation to roots (Johnson, 1990) like *Q. ellipsoidalis*, its slow growth strategy resulted in 56% lower total productivity as compared with its congener and 73% less productivity than *P. strobus* (Table 1). The idiosyncratic species impacts also extended to the SOM pool with differing impacts of species on different horizons of the soil profile (Table 1). This result suggests that SOM dynamics and belowground carbon storage potential associated with different species could be different at sites with deep soils. These results highlight the need for studies to extensively sample the SOM pool

when examining ecosystem carbon budgets, especially at deeper soil depths (Jackson *et al.*, 2002). As the majority of terrestrial carbon in a number of ecosystems is stored in the SOM pool (Schlesinger, 1997), if these deeper soil depths are not sampled adequately then an accurate ecosystem carbon budget may be difficult to determine. Additionally, as our results demonstrate, even small changes in the soil carbon pool can offset plant carbon gains and in turn reduce or eliminate the increases in total ecosystem carbon stocks by the fixation of atmospheric carbon into the plant carbon pool. Our findings also illustrate that in order to fully understand species impacts on the soil carbon pool we need to determine not only the size of soil carbon pool, but also the magnitude of the flux between the plant and soil carbon pools.

In conclusion, an understanding of species impacts on total ecosystem carbon stocks may provide novel sources of renewable carbon neutral biofuel and critical insights for mitigating rising concentrations of atmospheric CO₂. Our results demonstrate that the establishment of woody species can achieve both goals; however the balance between gains in plant carbon and loss of soil carbon is an important consideration when establishing any species for either objective. Our results also show that while grassland species may not be ideal for biofuel production relative to certain woody species, that particular grassland species may be more suitable in a carbon sequestration strategy. While all grassland species did not cause an increase in ecosystem carbon stocks, they were all carbon – neutral with plant carbon gains offsetting any loss of soil carbon. Although the establishment of certain grassland species did cause significant declines in soil carbon like those seen with *P. strobus*, but again this was a species-specific response. Based on their allocation patterns, *P. strobus* may be a more suitable candidate for biofuel production as compared with grassland species, while *Q. ellipsoidalis* may be an ideal species for sequestering carbon below-ground as compared with grassland species. Although our results are from short-term monocultures, and so they must be interpreted carefully, if the results from our experimental monocultures remain consistent, mixed pine-oak stands could achieve both management goals through short-term rotation (Sartori *et al.*, 2006; Dowell *et al.*, 2009) and selective harvest, with *P. strobus* being harvested for biofuel production and *Q. ellipsoidalis* being grown for terrestrial carbon sequestration. In order to implement successful management strategies towards either goal, species driven changes to both the plant and soil carbon pools must be examined (Guo *et al.*, 2007). Our study shows that species can have widely varying impacts on the major pools of carbon (plant and soil) which drive total ecosystem carbon

stocks, and that these species changes can be idiosyncratic and therefore species must be thoroughly examined before being implanted in any management strategy.

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