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Carbon Sequestration vs Agricultural Yields in Tree-Based Intercropping Systems as Affected by Tree Management

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Abstract

Tree-based intercropping (TBI) may increase C sequestration in agroecosystems, but reduce crop yields. In this study of TBI, we used *ecosys*, a comprehensive mathematical model of terrestrial ecosystems which represents interspecific competition for light, nutrients and water, to evaluate the concurrent effects of TBI on C sequestration and crop yields in TBI experiments conducted at St. Paulin and St. Edouard in southern Quebec. Total gains in C sequestration vs. total losses in crop yields over 11 years relative to monocropping were 682 vs 396 g C m⁻² at St. Paulin, and 841 vs 168 g C m⁻² at St. Edouard. These gains and losses were generally consistent with measurements at the two TBI sites, and with those at TBI experiments under similar environmental conditions elsewhere. Gains and losses depended on competition for light by trees

and crops, and so were affected by different fractions of tree foliage removal used to manage this competition in the model. The modelling protocol developed for this study provides a robust, process-based methodology to evaluate economic and environmental benefits of TBI under diverse climates, soils, and tree and crop management practices. Some of the key assumptions used to model TBI are discussed.

Key words: tree-based intercropping, agroforestry, interspecific competition, ecosystem modelling, ecosys

Introduction

Agroforestry can be defined as “a collective name for land use systems and technologies where woody perennials (trees, shrubs, palms, bamboos, etc.) are deliberately used on the same land management unit as agricultural crops and/or animals, either in some form of spatial arrangement or temporal sequence” (Thevathasan & Gordon 2004). Agroforestry combines knowledge, techniques and technologies that are used in both agriculture and forestry to create unified land-use systems (Meijer et al. 2015), which ostensibly provide economic and environmental to landowners. Agroforestry may consist of forested riparian buffers, windbreaks, tree-based intercropping (TBI), forest farming and silvopasture (Gao et al. 2014). The focus of this study was on TBI, where trees are planted in widely spaced rows among crops, thereby combining crop and tree production. This combination results in complex ecological and economic interactions between the trees and crops (Meijer et al. 2015).

During the past century, mechanization has led to the exclusion of trees from cropland (Gray 2000). As a result, there have been substantial losses of topsoil and soil organic carbon (SOC) from erosion, reduced plant litter production, reduced biodiversity over the landscape,

altered habitat and microclimate, and increased nutrient leaching (Thevathasan et al. 2012). Current temperate TBI systems were developed to reintroduce trees into agricultural landscapes, in an effort to counteract these losses (Bradley et al. 2008). TBI may offer substantial benefits over conventional monocropping systems, including timber production and carbon (C) sequestration, stabilization of topsoil thereby reducing erosion, increased biodiversity through habitat creation, improved nutrient and water cycling, improved water quality, enhanced snow and wind protection, and creation of a more favourable microclimate (Jose et al. 2004; Bradley et al. 2008).

Agroforestry is listed in the 5th IPCC report as having high potential for carbon sequestration by 2040 (Negash & Kanninen 2015). Carbon sequestration potential within temperate ecosystems has been estimated to be between 15 and 198 Mg C ha⁻¹ (Dixon et al., 1994). Nair and Nair (2003) proposed an overall estimate of 90 Tg C y⁻¹ for C sequestration in all agroforestry systems throughout the United States. While multiple forms of agroforestry are practiced across Canada, TBI is primarily located in Ontario and Quebec. At a TBI site in Ontario, Peichl et al. (2006) estimated that a hybrid poplar (*Populus deltoides* × *Populus nigra*) TBI sequestered 28 Mg C ha⁻¹ and a Norway spruce (*Picea abies*) TBI sequestered 7 t C ha⁻¹ relative to a monocrop over 13 years. Some of the sequestration by these TBIs was in soil, where SOC to a depth of 20 cm was 1.8 % and 1.6 % higher than in a monocrop over the same 13-year period (Oelbermann et al. 2006). Further C sequestration in TBI may occur deeper in the soil profile. After a further 12 years, C sequestration by these TBIs increased by a further 14.3 and 13.4 Mg C ha⁻¹ relative to a monocrop (Wotherspoon 2014). Therefore, agroforestry has an important role to play in increasing C sequestration, thereby moving toward more sustainable production systems (Montagnini & Nair 2004).

However TBI may reduce crop yields through competition with trees for light, nutrients and water. Competition for light is determined by the size and density of the tree crowns as determined by row spacing and orientation. If the tree crowns become too large or the tree rows are too narrow, the trees may limit radiation reaching the crops so that careful management of tree leaf area is required. In studies of temperate TBI systems, shading caused crop yield losses of up to 50% (Reynolds et al. 2007; Dufour et al. 2013). These losses may be greater in C_4 plants, which do not become light-saturated until near full sunlight, than in C_3 plants that become light-saturated at about half of full sunlight (Reynolds et al. 2007). Shading varies seasonally with deciduous trees, but is continuous with evergreens (Reynolds et al. 2007). As the trees grow larger, proper crown management such as regular trimming (typically removing 25-75 % of foliage every few years) is required to prevent the trees from completely overshadowing the crops as trees grow larger (Sato & Dalmacio 1991).

Competition for nutrients in TBI depends upon the distribution of tree and crop roots. Tree roots extend much deeper than do those of crops (Oelbermann et al. 2006; Wotherspoon 2014) and so can take up nutrients and water that are not accessible to crops. These nutrients may then be recycled back into the TBI ecosystem through litterfall, which can reduce the need to fertilize the intercropped area (Gao et al. 2014). Deeper tree roots may also reduce leaching of mobile nutrients such as nitrate (Bergeron et al. 2011; Link 2014) by as much as 28 % in high rainfall areas (Palma et al. 2007), reducing the need for fertilizer (Jose 2009; Gao et al. 2014). However tree roots will also compete with crop roots for nutrients and water within the crop rooting zone. In some TBI studies, nutrient competition has not been found to reduce crop yields (Miller & Pallardy 2001; Thevathasan et al. 2004). This competition is alleviated by fertilization in more intensively managed TBI systems.

Competition for water in TBI also depends upon the distribution of tree and crop roots. While water is not usually limiting in temperate ecosystems, agroforestry has both beneficial and detrimental hydrological effects. Because tree roots extend deeper into the soil, they have the ability to take up water that shallower crop roots cannot and therefore are able to recycle water that would otherwise be lost (Link 2014). Deeper tree roots also may enable hydrological lift, when water that is taken up from deeper, wetter soil is released into shallower drier soil, thereby increasing water available to crop roots (Ong et al. 2014). There is thus the potential for agroforestry to increase productivity in semiarid regions if seasonal excesses in precipitation allow deeper stores of water to develop (Ong et al. 2014). However, if deep water stores are not replenished, root competition for shallow water stores may occur, decreasing productivity in drier climates (Ong et al. 2014; Sudmeyer and Hall 2015). Since water tends not to be a limiting factor in temperate agriculture, competition for water in Canadian TBI may not be important.

The estimation of C sequestration in TBI is limited by the ability to measure changes in ecosystem C stocks over the time period of TBI experiments (Lorenz and Lal 2014), particularly those of tree roots, which are estimated to account for about one-third of total net primary productivity (NPP) by trees (Nair and Nair 2014). These estimates are difficult to compare among studies because of differences in tree and crop species, tree management, and measurement methodology. Ecosystem modelling can help to overcome these limitations. Most simulation of C sequestration by agroforestry systems is currently limited to models based on tree growth data from forests, such as CO₂FIX (Masera et al., 2003; Wotherspoon 2014). Agroforestry presents a challenge to such models, as they do not generally simulate tree-crop interactions (Luedeling et al. 2014; Nair and Nair 2014), so that effects on crop yields are overlooked (e.g., Palma et al. 2014; Negash and Kanninen 2015).

Currently, few options are available to accurately model SOC, tree shoot and root biomass, and crop yields in TBI systems (Luedeling et al. 2014). Such modelling requires detailed, mechanistic models that accurately represent the key processes by which different plant functional types (PFTs) compete for light, water and nutrients. This representation requires the explicit modelling of growth processes driving vertical distributions of leaf and root densities in each PFT. These densities must in turn drive light interception and water and nutrient uptake by each PFT from vertically dependent resources of light, water and nutrients within a common ecosystem. Light interception, and water and nutrient uptake must in turn drive the growth processes in each PFT by which these leaf and root distributions are determined. These processes are explicitly represented in the ecosystem model *ecosys*, which prognostically simulates multiple leaf and root layers in multi-specific plant biomes in which diverse plant and microbial populations compete for radiation, water, carbon, nitrogen, and phosphorus (Grant and Hesketh 1992; Grant 1994). *Ecosys* has been tested intensively and extensively for its ability to simulate C sequestration in multispecific forest (Grant et al. 2001, 2010; Dimitrov et al. 2014), grassland (Grant et al. 2012, 2016) and agricultural (Grant et al. 2007) systems, but has yet to be used in a multipurpose agroforestry system.

In this study, *ecosys* was used to study tree–crop interactions and their effects on tree and crop productivity in TBI experiments that were conducted from 2004 to 2014 at two sites (St. Paulin and St. Edouard) in Quebec, as part of the Agriculture Greenhouse Gases Program (AGGP) of Agriculture and Agri-Food Canada. Our objective was to determine:

- (1) the gain in C sequestered by TBI relative to monocropping due to the growth of woody perennials in TBI with continuous litterfall and extended growing seasons

- (2) the loss of crop yield in TBI relative to monocropping due to competition by woody perennials with crops for light, nutrients and water, and
- (3) how tree management (trimming) influences both (1) and (2).

Methods

A brief description of the St. Edouard and St. Paulin TBI sites and their experimental designs are given below, with further details available from Winans et al. (2014). Both research sites were converted to TBI in 2004 following conventional crop management. Subsequent plot management from 2004 to 2014 is given in Table 1 for both sites.

St. Paulin

The St. Paulin site (46° 27'N, 72° 59' W) was on a Dystric Brunisol (pH 6.2), classified as a loamy sand (790 g sand kg⁻¹, 160 g silt kg⁻¹ and 50 g clay kg⁻¹), with sections of sandy loam soil (560 g sand kg⁻¹, 300 g silt kg⁻¹ and 140 g clay kg⁻¹), which were mostly contained within one sampling block in the western section of the field. Mean annual temperature at the site is 4 °C, with annual precipitation of 1113 mm.

Treatments were established in 2004 according to a split-plot design, the whole-plot treatment being an annual crop rotation of buckwheat-canola-winter wheat (*Fagopyrum esculentum*-*Brassica napus*-*Triticum aestivum*) that was under-seeded to a clover/grass (*Trifolium arvense*/*Phleum pratense*/*Agropyron repens*) mix in 2009. Sub-plot treatments included the presence or absence of trees, including two clones of hybrid poplar (*Populus deltoides* W.Bartram ex Humphry Marshall x *P. nigra* L.), and two high-value hardwoods (red oak, *Quercus rubra* L.; black cherry, *Prunus serotina* Ehrh.). Tree rows were spaced 12 m apart with a northwest/southeast orientation, resulting in tree densities of 184 poplar stems ha⁻¹ and

130 hardwood stems ha^{-1} . Poplar and hardwoods were trimmed in 2004, 2005, and 2010 by removing part of the foliage to reduce shading of the TBI crop. Trimmed foliage was added to surface litter beneath the trees. Hardwoods were also trimmed in 2006 and 2007. On September 24-28 2012, two of every three poplars and one of every three hardwoods were thinned by removing the entire tree including roots. Horse manure was applied in 2004 and 2007, but no chemical fertilizers were used (Table 1).

St. Edouard

The St. Edouard experiment ($46^{\circ} 20' \text{ N}$, $73^{\circ} 11' \text{ W}$) was situated on a Humo-Ferric Podzol (pH 6.3), which was classified as a loamy sand ($860 \text{ g sand kg}^{-1}$, $120 \text{ g silt kg}^{-1}$ and $20 \text{ g clay kg}^{-1}$). Mean annual temperature is 3°C and annual precipitation is 1079 mm. While treatments were established with a similar design to that at the St. Paulin site, there were differences including: (i) high-value hardwoods were planted in 2001, poplars in 2004; (ii) trees were established in alternating rows of hybrid poplar/red oak or hybrid poplar/white or green ash (*Fraxinus americana* L., *F. pennsylvanica* Marsh.); (iii) tree rows were 10 m apart rather than 12 m; and (iv) the annual crop rotation consisted of buckwheat-canola with 2 years of fallow, which was then converted to a clover/grass mix in 2012; (v) chemical fertilizers were applied in 2005 and 2006 and cow manure in 2012 (Table 1). Tree rows followed a north-east/south west orientation, resulting in tree densities of 278 poplar stems ha^{-1} and 222 hardwood stems ha^{-1} , which were greater than those at St. Paulin. Poplar and hardwoods were trimmed in 2004, 2005, and again in 2010 by removing part of the foliage to reduce shading of the TBI crop. Trimmed foliage was added to surface litter beneath the trees. Hardwoods were also trimmed in 2006 and 2007. Trees were not thinned at this site.

Field Measurements

Light Interception in TBI

To estimate light interception by the trees in the TBI treatments, hemispherical photographs of the TBI canopy were taken skyward above the crop canopy using a fisheye lens (Nikon fisheye converter FC-E8, Tokyo, Japan) on a camera (Nikon Coolpix 990, Tokyo, Japan) that was placed 1 m above the ground at distances of 0, 1, 2, 3 and 6 m from the tree row along two transects in each of four plots at St. Paulin on 21 June 2012. These photographs produced circular images that recorded the size, shape, and location of gaps in the TBI overstory (Fig. 1). These images were most accurate when most of the pixels could be easily resolved into sky and non-sky classes, which meant waiting for dates with as little cloud cover as possible. The resulting images were converted into bitmaps and processed using the Gap Light Analyzer (GLA) program version 2.0, which transformed image pixel positions into angular coordinates, and then divided pixel intensities into sky and non-sky classes (Frazer et al. 1999). Once processed, the pixel groups were analyzed to estimate sky and non-sky fractions in each of the images. Averages and standard deviations of these fractions were then calculated for each distance from the tree row in all transects ($n=8$) to estimate the fraction of light intercepted with distance from the tree rows and its uncertainty.

Biometric Measurements in TBI and Monocropping

Measurements of diameters and heights of boles and branches were taken from 373 poplars and 129 hardwoods on 20 September 2012 at St. Paulin, shortly before thinning. These measurements were used to calculate tree biomass for this study from the allometric equations of Lambert et al. (2005) for hybrid poplars and hardwoods growing in natural forest stands in Canada. Tree biomass was also estimated at both sites in 2014 by Winans et al. (2016). At St. Paulin crop yields were measured at 1.5, 3.5 and 6 m from the trees rows in 2012 (Winans et al.,

2014) and at 1 and 6m in 2013. At St. Edouard crop yields were measured at 1 and 5 m from tree rows in 2013 and at 1.5, 3.0 and 4.5 m in 2014 All crop yield measurements were taken along two transects in each of four plots. On each sampling date, averages and standard deviations of yields were calculated for each distance from the tree row in all transects ($n=8$) to estimate crop yields and their uncertainties with distance from the tree rows in each TBI treatment on each measurement date. Crop yields were also measured on the same dates in monocropping treatments at both sites ($n=8$).

Estimates of crop and tree net primary productivity (NPP) for poplar TBI systems in Quebec were conducted by Winans et al. (2015). Vertical profiles of crop and tree root length density were measured at St. Paulin in July 2011 by Bouttier et al. (2014). Tree and crop litterfall was measured at both sites in 2014 by Winans et al. (2016). Changes in soil organic C were estimated by Winans et al. (2015) for TBI vs monocropped hay in southern Quebec. Total C sequestration from 2004 to 2014 was estimated at St. Paulin and St. Edouard by Winans et al. (2016).

Model Experiment

Model Description

Ecosys is a mathematical model of terrestrial ecosystems noted for the comprehensiveness of its component processes and the detail to which they are represented. This detail allows ecosystem processes to be modelled from the basic stoichiometry, energetics and kinetics of energy, C, N and P transformations derived from independent, well-constrained experiments. The model thus integrates basic findings from component disciplines (biometeorology, plant biology, soil biology, soil physics, soil chemistry, agronomy) into an

integrated framework for studying complex ecosystem behaviour. The simulation of processes governing gross primary productivity (GPP), autotrophic and heterotrophic respiration (R_a and R_h) and, hence those of water and nutrient cycling and of net ecosystem productivity (NEP) most relevant to this study, has been widely described and tested in papers cited in the Introduction. Key algorithms for these processes are published in online Supplements that accompany these papers. Those model processes that are particularly relevant to simulating interspecific competition for light, nutrients and water are described in further detail below.

Light Competition

Competition for light is modelled from light intercepted by leaves and stems of each PFT in successive layers of an aggregated canopy from top to bottom for incoming direct and diffuse radiation, and from bottom to top for backscatter radiation. Interception in each canopy layer is calculated in 3-dimensional space (azimuth, inclination) accounting for leaf optical properties (albedo, transmissivity) and self-shading (clumping factor). The leaf area of each PFT in each layer is calculated from the extension of internodes, petioles and leaves that is driven by the allocation of non-structural C, N and P to each organ of each PFT (Grant et al. 1989; Grant and Hesketh 1992; Grant 1994). Rates of allocation are determined by concentration gradients of non-structural C, N and P within each PFT. These gradients arise from production by leaf CO_2 fixation, which is determined in part from light interception, and by root N and P uptake, which is determined in part from root density, versus consumption by R_a in each organ, as determined by its nutrient and water status. Leaf areas aggregated from all PFTs are divided at the start of each hourly time step of the model into 10 layers of equal LAI for calculating light interception, so that perennial woody plants that accumulate C, N and P in stems (trees), eventually shade

annual (grain crops) and perennial non-woody plants (forages) that regrow from the ground up each year (Fig. 2).

Nutrient and Water Competition

Competition for soil nutrients and water depends upon nutrient and water uptake by each PFT from common nutrient and water stocks held in a multilayer soil profile (Fig. 2). These stocks are determined by algorithms for transformations and transfers of soil C, N and P, and for transfers of soil water described in detail elsewhere (e.g. Grant, 2013; Grant et al., 2007, 2016). Uptake depends upon root length density of each PFT in each soil layer, which in turn depends on extension of primary (vertical) and secondary (horizontal) root axes that are driven by the allocation of non-structural C, N and P to each axis as enabled by its nutrient and water status (Grant 1993a,b, 1998). Extension by each PFT is calculated on a per plant basis and then aggregated to the population. Therefore larger perennial woody plants with greater shoot-root transfers per plant maintain deeper root length density profiles than do smaller perennial non-woody plants (forages), and annual plants (crops), for which extension must start at seeding depth with each planting. As was the case for aboveground organs, rates of allocation are determined by concentration gradients of non-structural C, N and P within each PFT arising from production by leaf CO₂ fixation, and by root N and P uptake versus consumption by R_a in each axis determined by its nutrient and water status.

Model Runs

Model Spinup Run

Ecosys was initialized on 1 January of the model year 1954 with key properties for the soil profiles of the Dystric Brunisol at St. Paulin and the Humo-Ferric Podzol at St. Edouard

taken from the Soil Landscapes of Canada v. 3.2 (SLC 2010) to a depth of 1 m. The model was seeded with a clover/grass mixture in the spring of 1954 with the biological properties for clover and grass functional types (C_3 perennial legume/non-legume) used in Grant et al. (2016). The model was then run for five cycles of 10 years under a ten-year sequence of weather data taken from the North American Regional Reanalysis (NARR) from 2001 to 2010 (Wei et al. 2014) for the grid cell in which each site was located. The clover/grass was terminated at the end of each cycle, reseeded at the start of the following cycle, and harvested twice yearly between, thereby representing the land use histories of the sites. The spinup run thus ended at 31 December of the model year 2003, by which time C, nutrient and water cycling in the model had equilibrated under site conditions and land management practices prior to the production runs.

Model Production Runs

Crop Management

The model spinup run was then continued from 1 January 2004 to 31 December 2014 with weather data from NARR for 2004 to 2010, and from information that was posted by Environment Canada (http://climate.weather.gc.ca/index_e.html) for local weather stations from 2011 to 2014. The rotations at each site (Table 1) were implemented using crop functional types representing buckwheat, canola, winter wheat (C_3 annual non-legumes) and clover/grass mixture (C_3 perennial legume (symbiotic N_2 fixer) / C_3 perennial non-legume), the attributes of which were the same as those used for these functional types in previous studies (e.g., Grant et al. 2007, 2012, 2016). Annual crops were seeded and harvested on dates corresponding to those in the field, at which time all grain biomass was removed, and remaining shoot and root biomasses were added to surface and soil litter. Clover/grass was cut twice each year on dates

corresponding to local practice at a height of 0.05 m at which time 90% of shoot biomass above this height was removed and 10% was added to surface litter. After cutting, regrowth was driven by remaining LAI and partial remobilization of stored reserves (Grant et al. 2016).

Tree Management

TBI treatments modelled at both sites included a tree functional type representing a deciduous growth habit for both the poplar and hardwoods, attributes of which were the same as those used in previous studies (e.g., Grant et al. 2010; Grant 2013). The effects of tree spacing on tree-crop competition were represented in the model by a zone of direct competition between trees and crops for common resources of light, nutrients and water that extended from 0 to 2 m from the centre of the tree row (Fig. 2). The remainder of the TBI treatment was represented by a zone of indirect competition 2 to 6 m (St. Paulin) or 2 to 5 m (St. Edouard) from the centre of the tree row, thereby accounting for the 12 m and 10 m row spacing at these sites. These zones were fully connected, allowing water and nutrients to be exchanged laterally between the 0–2 m zone and the 2–6 or 2–5 m zone so that although no shading was modelled in these latter zones, nutrients and water uptake by crops could be affected by those of trees in the adjacent 0–2 m zone. The 0–2 m zone of direct competition was taken from the results of Gao et al. (2013), who found reductions in PAR, CO₂ fixation and crop yields that extended to 1.5 m, but not to 2.5 m, from rows of 4- to 5-year-old unpruned apple (*Malus pumila* M.) trees.

The modelled trees were trimmed in years corresponding to those in the field study (Table 1) using a value for the fraction of foliage removed from all canopy layers (trimming fractions) of 0.50 at St. Paulin and 0.67 at St. Edouard where tree populations were larger and row spacing smaller (sec. 2.2). Trimmed foliage was added to surface litter. The model also used

a value for reducing the clumping factor with each trimming of 0.025 at St. Paulin and 0.05 at St. Edouard from its initial value of 0.7 for deciduous trees (He et al. 2016) to account for the increase in self-shading caused by reduction of the canopy volume with smaller branch lengths from trimming. These trimming fractions allowed the model to simulate tree light interception that corresponded to the non-sky fraction measured on 21 June 2012 at St. Paulin (section 2.3) and to estimates of this fraction at St. Edouard. References to trimming fractions in the text below include associated reductions in the clumping factor. Modelled trees were thinned at St. Paulin on 26 Sept. 2012, and thinned trees were completely removed, as in the field experiment (Section 2.1, Table 1).

Model Production Runs with Altered Tree Trimming

A key purpose of the model experiment, as stated in the Introduction, was to determine how tree management, represented by trimming fraction, determined the extent to which gains in TBI C stocks offset losses in TBI crop yields. To evaluate different tree trimming fractions on gains in C stocks vs losses in crop yields, two alternative model runs were conducted using smaller or larger values for trimming fractions and reductions in the clumping factors than those used in the production run (0.33 and 0.0 or 0.75 and 0.05 at St. Paulin; 0.50 and 0.025 or 0.83 and 0.1 at St. Edouard). Larger (smaller) trimming fractions left less (more) tree leaf area and therefore reduced (increased) shading of the TBI crop. All other inputs (weather, land management, crop rotation) in these scenarios remained unchanged.

Results

Light Interception in TBI

Light intercepted by trees in the modelled TBI treatments was compared with the fraction of sky covered by trees measured with the GLA program at St. Paulin on 27 July 2011 (Winans et al., 2014) and 21 June 2012 (Table 2a). Interception modelled in the 0 – 2 m zone was greater than the tree sky fraction measured at 0 and 1 m from the tree rows on both dates. However no interception was modelled in the 2 – 6 m zone whereas a small tree sky fraction was measured at 3 and 6 m from the tree rows. The resolution of the TBI into shaded and non-shaded zones thus allowed the model to approximate differences in shading with distance from tree rows.

Light interception by trees in the model increased with less foliage removal from smaller trimming fractions, and decreased with more foliage removal from larger trimming fractions (Table 2b). These differences in interception were caused by the direct effects of foliage removal on LAI and by the effects of LAI on subsequent forest regrowth. Interception modelled at St. Paulin decreased in 2013 from that in 2012 after thinning later in 2012 (Table 1). Interception modelled at St. Edouard increased in 2013 with undisturbed tree growth.

Crop Yields and Tree Growth in TBI vs Monocropping

St. Paulin

Shading by trees (Table 2) reduced crop yields modelled in the 0 – 2 m zone from those in the 2 – 6 m zone and in the monocrop (Table 3a). This modelled reduction was larger in 2012 before tree thinning than in 2013 after tree thinning, although the corresponding reduction measured at 1.5 m vs. 3 and 6 m from the tree rows in 2012 was smaller. Yields modelled and measured in the 2 – 6 m zone did not differ significantly from those in the monocrop, indicating that crops in this zone were not affected by shading from trees (Table 2a). Aboveground tree biomass modelled on 20 September 2012, shortly before thinning (Table 1) was larger than, but

within the range of, tree biomass calculated from diameter and height measurements taken on this date.

St. Edouard

Shading by trees caused reductions in crop yields modelled in the 0 – 2 m zone from those in the 2 – 5 m zone that were greater than those measured at 1.5 m vs. 3 and 4.5 m from the tree rows (Table 3b). Yields measured at 3 and 4.5 m from the tree rows were smaller than those in the monocrop, indicating that shading may have affected crop growth in this zone, although measurement uncertainties were large.

Annual C Budgets for TBI vs Monocropping

St. Paulin

Annual C budgets were taken from model results for TBI and monocropping at both sites during the last year of the study in 2014. At St. Paulin, trees contributed substantially to TBI GPP and NPP within the 0–2 m zone, but caused a large reduction in clover/grass GPP and NPP compared to that in the 2–6 m zone and the monocrop (Table 4). The contribution to GPP and NPP by trees exceeded the losses in GPP and NPP by crops, so that total weighted GPP and NPP in TBI (1259 and 652 g C m⁻² y⁻¹) exceeded those in the monocrop (1044 and 530 g C m⁻² y⁻¹).

About one-fifth and one-third of NPP modelled for trees and crops respectively was invested in roots (Table 4). This investment drove vertical profiles of root length density for the larger but less populous hardwood and poplar trees that were deeper but less dense than those for the smaller but more populous clover/grass plants (Fig. 3). Reductions in clover/grass shoot NPP due to shading by trees in the 0 – 2 m zone caused commensurate reductions in clover/grass root NPP (Table 4), and hence decreases in vertical profiles of root length density with TBI (Fig. 3).

TBI raised NEP in the model by increasing NPP relative to R_h . TBI raised total NPP substantially in the 0–2 m vs. 2–6 m zone and the monocrop (880 vs. 539 and 530 g C m⁻² y⁻¹), but raised R_h only slightly (420 vs. 386 and 384 g C m⁻² y⁻¹), so that NEP (= NPP – R_h) modelled in the 0–2 m zone was substantially greater than those in the 2–6 m zone and the monocrop (460 vs. 149 and 147 g C m⁻² y⁻¹) (Table 4). Consequently greater soil respiration ($R_s = R_h + \text{root } R_a$) was modelled in the 0–2 m TBI zone (716 g C m⁻² y⁻¹) than in the 2–6 m zone and the monocrop (665 and 661 g C m⁻² y⁻¹).

In the model, TBI maintained greater SOC than did monocropping by increasing litterfall relative to R_h . Total litterfall was greater relative to R_h in the 0–2 m zone (375 vs 420 g C m⁻² in Table 4) than in the 2–6 m zone (303 vs 386 g C m⁻²) and monocrop (299 vs 384 g C m⁻²), causing smaller loss of SOC (- 45, -83 and -85 g C m⁻² y⁻¹, respectively) to be modelled during 2014 at St. Paulin.

TBI raised NBP (= NEP – harvest) by increasing NEP and reducing crop removals (Table 4), thereby causing a substantial C sink to be modelled in the 0–2 m zone (361 g C m⁻² y⁻¹), but a small source in the 2–6 m zone and in the monocrop (-69 and -72 g C m⁻² y⁻¹). The C budget modelled in the 2–6 m zone was similar to that in the monocrop, indicating that very little indirect competition between trees and crops was modelled more than 2 m away from the tree rows.

The loss of dissolved inorganic nitrogen (DIN) modelled in the 0–2 m TBI zone (0.04 g N m⁻² y⁻¹) was smaller than that on the 2–6 m zone (0.23 g N m⁻² y⁻¹), which in turn was slightly smaller than that in the monocrop (0.25 g N m⁻² y⁻¹), indicating greater nutrient retention by the deeper-rooted trees (Fig. 3).

St. Edouard

Annual C budgets taken from model results for TBI and monocropping at St. Edouard in 2014 (Table 5) indicated tree - crop interactions similar to those at St. Paulin (Table 4). TBI raised total GPP and NPP in the 0–2 m zone (1538 and $805 \text{ g C m}^{-2} \text{ y}^{-1}$) from those in the 2–5 m zone (993 and $527 \text{ g C m}^{-2} \text{ y}^{-1}$) and the monocrop (986 and $523 \text{ g C m}^{-2} \text{ y}^{-1}$), but reduced GPP and both shoot and root NPP of clover/grass. TBI raised R_h only slightly in the 0 - 2 m zone (324 vs. 291 and $290 \text{ g C m}^{-2} \text{ y}^{-1}$), so that NEP in the 0-2 m zone ($477 \text{ g C m}^{-2} \text{ y}^{-1}$) was greater than those in the 2–5 m zone and monocrop (237 and $233 \text{ g C m}^{-2} \text{ y}^{-1}$). Total litterfall was greater relative to R_h in the TBI 0–2 m zone (336 vs. $324 \text{ g C m}^{-2} \text{ y}^{-1}$) than in the 2 - 5 m zone (259 vs. $291 \text{ g C m}^{-2} \text{ y}^{-1}$) and monocrop (259 vs. $290 \text{ g C m}^{-2} \text{ y}^{-1}$) (Table 4), indicating greater gain of SOC ($+12$, -32 and $-31 \text{ g C m}^{-2} \text{ y}^{-1}$, respectively).

TBI raised NBP by increasing NEP while reducing crop removals, causing a substantial C sink to be modelled in the 0–2 m zone ($410 \text{ g C m}^{-2} \text{ y}^{-1}$), but only a small sink in the 2–5 m zone and the monocrop (46 and $46 \text{ g C m}^{-2} \text{ y}^{-1}$). C budgets modelled in the 2–5 m TBI zone were similar to those in the monocrop, indicating that very little indirect competition between trees and crops was modelled more than 2 m away from the tree rows.

As at St. Paulin, the loss of DIN modelled in the 0–2 m TBI zone ($0.04 \text{ g N m}^{-2} \text{ y}^{-1}$) was smaller than that in the 2–5 m zone ($0.82 \text{ g N m}^{-2} \text{ y}^{-1}$), which in turn was slightly smaller than that in the monocrop ($0.87 \text{ g N m}^{-2} \text{ y}^{-1}$). This response indicated greater soil nutrient retention by the deeper-rooted trees in the model (e.g. Fig. 3).

Effects of Trimming Fractions on Crop Yield Losses in TBI vs Monocropping

Gains in GPP, NPP, NEP and NBP and losses in crop yields in TBI vs monocropping (Tables 3, 4 and 5) were affected by the fractions of foliage removed with each trimming during the course of the modelled TBI experiment. As this experiment progressed, smaller trimming fractions increased light interception by trees (Table 2b) and hence reduced light interception by crops, causing smaller crop yields (Fig. 4). Crop yield reductions modelled in the 0–2 m TBI zone (Table 3) increased with tree growth from 2004 to 2014 (Fig. 4a,d), except in 2013 at St. Paulin following tree thinning in September 2012 (Table 1). Crop yields modelled in the 2–6 m TBI zone at St. Paulin and the 2–5 m TBI zone at St. Edouard remained close to monocrop values for all trimming fractions throughout the study period (Fig. 4b,e), indicating limited effects of indirect competition on crop yield in TBI caused by the absence of shading (Table 2b).

Effects of Trimming Fractions on Total C Sequestration in TBI vs Monocropping

St. Paulin

Different trimming fractions greatly affected tree growth as well as crop yields, and so affected C sequestration. Smaller trimming fractions caused total NPP modelled from 2004 through 2014 at St. Paulin to rise (Table 6), because increased tree productivity from increased light interception (Table 2b) was only partly offset by reduced crop productivity from reduced light interception (Fig. 4). Smaller trimming fractions had little effect on R_h and so caused NEP to rise sharply. However larger trimming fractions increased crop productivity from increased light interception, and so caused larger crop harvest removals (Fig. 4) that exceeded NEP when trimming fractions were 0.50 or greater (Table 6). The amount of tree biomass removed by thinning in 2012 declined with increased trimming fractions because consequent reductions in tree LAI slowed subsequent tree growth. Crop harvest removals were largely offset by additions of manure (Table 1) and of non-structural C, N and P used to seed trees and crops. Consequently,

total NBP that was simulated from 2004 through 2014 with the management practices St. Paulin (Table 1) indicated that TBI would be a substantial C sink with a trimming fraction of 0.33 (979 g C m^{-2}), but that this sink would decline with trimming fractions of 0.50 and 0.67 (764 and 475 g C m^{-2}) while monocropping would be close to carbon-neutral (82 g C m^{-2}).

The increased C sequestration modelled in TBI vs monocropping was mostly attributed to gains in above and belowground tree (poplar + hardwood) biomass (Table 6). Aboveground tree biomass modelled in 2014 had been reduced considerably by thinning (Tree Removal in Table 6) from that modelled and measured in 2012 (Table 2), but partially regrew during the following two years. However, the gains in modelled tree biomass declined sharply with increased trimming fractions (Table 6). The gains in tree biomass in TBI vs monocropping were partly offset by losses in belowground crop biomass (clover + grass roots), which rose with increased shading from reduced trimming.

The increased C sequestration modelled in TBI was also partly attributed to small gains in SOC through the soil profile relative to monocropping (apparent as smaller losses in Table 6) because total litterfall modelled in TBI was larger relative to R_h (Table 4). However, these gains in SOC with TBI declined with greater trimming fractions because of reduced tree litterfall.

In the model run with a trimming fraction of 0.50, TBI enabled a gain of $682 (= 764 - 82) \text{ g C m}^{-2}$ in C sequestration (NBP) at a cost of $398 (= 2088 - 1690) \text{ g C m}^{-2}$ in crop yields relative to monocropping for the management practices at St. Paulin from 2004 through 2014 (Table 6). Changes in NBP vs crop yields modelled with increased trimming (Table 6) indicated that losses/gains in C sequestration exceeded gains/losses in crop yields by a ratio of about 2:1 g C g C^{-1} for the increases/decreases in trimming fractions that were implemented in the alternative

tree management scenarios. Total losses of DIN also increased with TBI trimming fractions and with monocropping (Table 6).

St. Edouard

Total NPP modelled from 2004 through 2014 at St. Edouard (Table 7) was less than that at St. Paulin (Table 6) because there were two fallow years with no crop production, and because perennial clover/grass mix was introduced three years later in 2012 vs 2009 without being underseeded in an annual crop (Table 1). Smaller trimming fractions also caused total NPP at St. Edouard to rise (Table 7) because increased tree productivity with increased light interception (Table 2b) was only partly offset by decreased crop productivity with reduced light interception (Fig. 4). However R_h rose only slightly with smaller trimming fractions so that NEP rose sharply. Total crop harvest removal was close to NEP with the smallest trimming fraction, but exceeded it with larger ones. Additions of C with manure (Table 1) and seeding failed to offset the excess of harvest removal over NEP for the largest trimming fraction and the monocrop. Consequently, TBI with the management practices implemented from 2004 to 2014 at St. Edouard was modelled as a C sink with trimming fractions of 0.50 and 0.67 (398 and 119 g C m^{-2}), and as a C source with a trimming fraction of 0.83 (-376 g C m^{-2}) and with monocropping (-723 g C m^{-2}) (Table 7).

As at St. Paulin, increased C sinks modelled in TBI vs monocropping were attributed mostly to gains in above- and belowground tree biomass, which declined with reduced light interception from increased trimming. Modelled aboveground tree biomass (poplar + hardwood) was greater than that at St. Paulin (Table 6) despite larger trimming fractions, because tree populations at St. Edouard were larger (sec. 2.2) and no tree thinning was carried out. The gains in tree biomass in

TBI were partly offset by reductions in belowground crop (clover/grass) biomass. These reductions rose with increased shading from reduced trimming.

C sequestration in tree + crop biomass was offset by substantial declines in SOC at this less intensively managed site (Table 1). These declines were slightly smaller in TBI because total litterfall was greater relative to R_h (Table 5), indicating small gains in SOC relative to monocropping. However, these gains declined with increased trimming because of reduced tree litterfall.

In the production run with a trimming fraction of 0.67, TBI enabled a gain of 842 ($= 119 - [-723]$) g C m⁻² in C sequestration (NBP) at a cost of 155 ($= 1073 - 918$) g C m⁻² in crop yields relative to monocropping for the management practices at St. Edouard from 2004 through 2014 (Table 7). Changes in NBP vs crop yields that were modelled with increased trimming, indicated that losses/gains in C sequestration exceeded gains/losses in crop yields by a ratio of about 4:1 g C g C⁻¹ for the increases/decreases in trimming fractions that were implemented in the alternative tree management scenarios. This ratio was larger than that at St. Paulin because tree populations were larger and crop yields were smaller. As at St. Paulin, total losses of DIN also increased with TBI trimming fractions and with monocropping (Table 7).

Discussion

Comparison of Results with Other TBI Studies

Crop and Tree Productivity

Values for NPP modelled in TBI vs. monocropping at St. Paulin and St. Edouard were comparable to those published earlier at these sites and at similar sites elsewhere. The area-weighted tree NPP modelled for TBI in 2014 of 199 g C m⁻² y⁻¹ at St. Paulin ($= [480 + 116] \times 2/6$

from Table 4) and of $223 \text{ g C m}^{-2} \text{ y}^{-1}$ at St. Edouard ($= [548 + 10] \times 2/5$ from Table 5) were within the range of 159 to $363 \text{ g C m}^{-2} \text{ y}^{-1}$ estimated for low- and high-yielding poplar in TBI systems in Quebec by Winans et al. (2015). The area-weighted clover/grass NPP modelled for TBI in 2014 of $454 \text{ g C m}^{-2} \text{ y}^{-1}$ at St. Paulin ($= 284 \times 2/6 + 539 \times 4/6$ from Table 4) and of $415 \text{ g C m}^{-2} \text{ y}^{-1}$ at St. Paulin ($= 247 \times 2/5 + 527 \times 3/5$ in Table 5) were smaller than a hay NPP of $755 \text{ g C m}^{-2} \text{ y}^{-1}$ estimated for TBI in southern Quebec by Winans et al. (2015), who assumed no reduction of hay productivity in TBI vs monocropping.

Reductions of crop NPP modelled in TBI vs. monocropping caused reductions in crop yields of 15–20 %, all of which was modelled in the 0–2 m TBI zone. These losses were consistent with losses in soybean yields of ca. 50 % measured 2 m from trees, and with differences in soybean yields of -25 % to +25 % measured 6 m from trees by Reynolds et al. (2007) in a 10- to 11-year-old TBI experiment in southern Ontario.

Plant and Soil C Stocks

The aboveground tree biomasses modelled at the end of 2014 were smaller than the estimate of 3000 g C m^{-2} derived by Winans et al. (2016) for 10 year-old TBI at St. Paulin, although the value modelled in our study excluded foliage. However, the biomasses modelled after 10 years with the smallest trimming fractions were consistent with estimates of aboveground wood growth from 60 to $100 \text{ g C m}^{-2} \text{ y}^{-1}$ for hybrid poplar intercropped with hay in southern Quebec by Winans et al. (2015), and from 100 to $120 \text{ g C m}^{-2} \text{ y}^{-1}$ for hybrid poplar intercropped with annuals in southern Ontario by Peichl et al. (2006) and Wotherspoon (2014).

The very small gains in SOC modelled to a depth of 1 m in TBI vs. monocropping at both sites were consistent with the findings of Winans et al. (2014) that increases of soil C and N stocks in the topsoil (0 – 30 cm) of TBI relative to monocropping at could not be measured at

St. Paulin and St. Edouard in 2012. Although modelled gains in TBI SOC were greater in the 0 – 2 m zones at both sites, measurable gains in SOC under TBI would likely require much longer periods than that of this study, given the sparse tree populations used in TBI.

C Sequestration

The modelled gains in C sequestration at St. Paulin and St. Edouard were 682 g C m^{-2} and 842 g C m^{-2} relative to monocropping after 11 years in TBI with trimming fractions of 0.50 and 0.67. These gains were less than one of 2800 g C m^{-2} in a poplar TBI, but similar to one of 700 g C m^{-2} in a Norway spruce (*Picea abies* [L.] H.Karst) TBI, estimated by Peichl et al. (2006) after 13 years at Guelph, ON. Gains in NBP modelled in 2014 at both sites for TBI in the 0–2 m zone vs monocropping were comparable to gains in C sequestration of 207 vs. $-136 \text{ g C m}^{-2} \text{ y}^{-1}$ that were calculated for a poplar–soybean (*Glycine max*) TBI vs soybean monocrop at Guelph, ON, by Wotherspoon (2014), where C sequestration by annual soybean at Guelph would be less than that by perennial grass/clover in this study. However this gain in C sequestration was much smaller than ones of 5349 and 7730 g C m^{-2} estimated by Winans et al. (2016) after 10 years of TBI at St. Paulin and St. Edouard, based on calculations of tree biomasses that were much larger than those modelled here.

Nitrate Leaching and Root Growth

Reductions in nitrate leaching modelled with TBI vs. monocropping at both sites were smaller than those found experimentally at St. Edouard by Bradley et al. (2008), but were consistent with reductions of up to 28% modelled by Palma et al. (2007). These reductions were enabled by deeper root length density profiles modelled for trees vs. crops. These profiles at St. Paulin were comparable to those presented in Figs. 3 and 4 of Bouttier et al. (2014) who measured poplar roots to a depth of 1 m but clover/grass roots only to a depth of 0.5 m in July 2011 at St. Paulin. Bouttier et al. (2014) found that clover/grass root length densities (RLD) were

much greater than those of poplar, but were reduced under TBI vs. monocropping as also modelled in this study. The tree and clover/grass root biomasses modelled at both sites were consistent with root:shoot ratios estimated for TBI systems of ~ 0.2 for hybrid poplar (Thevathasan and Gordon 2004; Peichl et al. 2006) and 1.67 for hay (Bolinder et al., 2007).

Modelling Productivity and C Sequestration in TBI Systems

The modelling protocol described here realizes the three objectives in the Introduction by providing a robust, process-based means of modelling gains in C sequestered by TBI relative to monocropping due to the growth of woody perennials, and the accompanying losses in crop yields due to competition by woody perennials with crops for resources, as affected by climate, soil and tree management. This modelling was based on an explicit simulation of interspecific competition for light, water and nutrients in multispecific vertical profiles of leaf area and root length that directly affected uptake of CO_2 , water and nutrients by each species. This modelling represents an advance on earlier efforts to model TBI in which parameters for tree and crop growth were directly calibrated from yield tables (e.g. Palma et al., 2007), and interspecific competition was represented by dimensionless growth modifiers (e.g. Masera et al., 2003).

A key assumption upon which the present protocol is based is the 0–2 m zone from the centre of the tree row within which the effects of competition for light, nutrients and water were modelled. This assumption enables the model to approximate the effects on competition of distance from tree rows. The size of this zone was inferred from earlier TBI experiments (e.g., Gao et al., 2013), and is likely adequate to represent nutrient and water competition. However as trees grow taller, this zone is likely to become too small to represent shading, particularly in E-W tree rows. Measurements of irradiance by Reynolds et al. (2007) indicated that shading at 6 m

from tree rows was not apparent with N-S rows of 8 metre-tall silver maple (*Acer saccharinum* L.), but was important with those of 12 metre-tall hybrid poplar. Results from TBI experiments clearly indicate that the intensity of tree-crop competition declines with distance from the tree rows, indicating the need for different zones of competition in TBI modelling. At the current stage of model development, shading of crops by trees outside of the zone of direct competition (0 – 2 m in this study) as affected by solar angle and tree row orientation, is not accounted for. However the size of these competition zones can readily be changed in *ecosys* model runs, so that the effects of larger sizes could be explored for TBI with larger trees.

In this modelling study, crop nutrient status was indicated by foliar N concentration arising from NH_4^+ and NO_3^- uptake by roots relative to CO_2 fixation by foliage (Grant, 2013; Grant et al., 2016), and crop water status was indicated by foliar water potential arising from water uptake by roots vs transpiration by foliage (Grant et al., 2007). These indicators were not adversely affected by competition with trees in the 0 – 2 m zones at either site. Therefore losses of crop yields in the model were attributed entirely to competition for light, rather than for nutrients and water, as was also inferred by Bouttier et al. (2014) from observations at St. Paulin. The absence of competition for nutrients and water was attributed in the model to lower nutrient and water uptake requirements by shaded, slower-growing crops with lower fixation and transpiration rates. The field experiment that was modelled in this study included applications of manure and fertilizer (Table 1), and occurred in a climate zone with precipitation that exceeded evapotranspiration. These model findings would likely have been different under a drier climate or less fertile soil in which competition for water or nutrients would be greater. The process-based approach used here to model competition allows such conditions readily be modelled from changes in inputs for weather, soil properties and nutrient amendments.

Yield losses modelled in TBI increased with tree growth as the model runs progressed, indicating that these losses were sensitive to tree canopy size. Consequently, model results were very sensitive to tree trimming fractions, for which model values of 0.50 at St. Paulin and 0.67 at St. Edouard were inferred from measurements of light interception by TBI trees that were conducted as part of this study. Light interception modelled with these fractions in the 0 – 2 m zones was similar to that measured by Reynolds et al. (2007) over soybeans in a 10-year-old TBI experiment at Guelph, and by Bouttier et al. (2014) after 8 years of TBI at St. Paulin. However, modelled interception was sensitive to the values selected for trimming fractions and the accompanying reduction in clumping factors, both of which can be established from independent measurements, but are not in practice. Changes in trimming fractions had important effects on the ecological vs. economic productivity of TBI systems in the model. Increasing/decreasing trimming fractions were shown to decrease/increase C sequestration by 2 – 4 g C for each increase/decrease of 1 g C in crop yield, depending on tree and crop management practices. These ratios indicated that trimming fractions should be determined by the comparative values of wood production plus C sequestration vs. crop production of a TBI system, with smaller or larger values when tree or crop production is more valuable. These comparative values could be established from the monetary return from C retained in ecosystems vs that removed in crops to establish the economic as well as the ecological viability of TBI as affected by tree management. Further details of such analyses are given in Winans et al. (2015, 2016). Future TBI research should therefore focus on the measurement of trimming fractions and their effects on canopy optical properties and light interception.

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Table 1. Crop rotation, fertilizer use, land and tree management at St. Paulin & St. Edouard for 2004-2014

St. Paulin	Year	Crop	Fertilizer	Management	Tree Management
	2004	oat	30 Mg ha ⁻¹ horse manure	disc till	poplar and hardwoods planted at 184 and 130 ha ⁻¹
	2005	buckwheat		disc till	all trees trimmed
	2006	buckwheat		disc till	hardwood trimmed
	2007	canola	30 Mg ha ⁻¹ horse manure	disc till	hardwood trimmed
	2008	buckwheat/ winter wheat		disc till	
	2009	winter wheat/ clover/grass		disc till	
	2010	clover/grass			all trees trimmed
	2011	clover/grass			
	2012	clover/grass	5 Mg ha ⁻¹ lime		2/3 poplar, 1/3 hardwood thinned and removed
	2013	clover/grass			
	2014	clover/grass			
St. Edouard	Year	Crop	Fertilizer	Management	Tree Management
	2001				hardwoods planted at 222 ha ⁻¹
	2004	buckwheat		disc till	poplar planted at 278 ha ⁻¹
	2005	buckwheat	7.6 g N m ⁻²	disc till	all trees trimmed
	2006	buckwheat	8.2 g N m ⁻² + 3.4 g P m ⁻²	disc till	hardwood trimmed
	2007	canola	5 Mg ha ⁻¹ lime	disc till	hardwood trimmed
	2008	canola			
	2009	fallow		fallow	
	2010	fallow		fallow	all trees trimmed
	2011	buckwheat		disc till	
	2012	clover/grass	10.8 Mg ha ⁻¹ cow manure		
	2013	clover/grass			
	2014	clover/grass			

Table 2. (a) Fraction of incoming radiation intercepted by the modelled trees in 0 – 2 m and 2 – 6 m zones of the tree-based intercropping (TBI) treatment (trimming fraction = 0.50), and fraction of sky covered by trees measured with Gap Light Analyzer (GLA) program version 2.0 near midday on 27 July 2011 by Winans et al. (2014) and on 21 June 2012 for this study at St. Paulin and (b) fraction of incoming radiation intercepted by the modelled trees in 0 – 2 m zones with different trimming fractions at St. Paulin and St. Edouard on 21 June 2012 and 2013.

(a)

Year	Date	Zone	Modelled	Measured
2011	27 July	0 – 2	0.69	0.41 ± 0.17^a
		2 – 6	0.00	0.15 ± 0.04^b
2012	21 June	0 – 2	0.66	0.42 ± 0.17^a
		2 – 6	0.00	0.16 ± 0.07^b

^a average of values measured at 0 and 1 m from tree rows

^b average of values measured at 3 and 6 m from tree rows

(b)

Site	Year	Trimming Fraction		
St. Paulin		0.33	0.50	0.75
	2012	0.81	0.66	0.51
	2013	0.66	0.45	0.27
St. Edouard		0.50	0.67	0.83
	2012	0.60	0.48	0.23
	2013	0.62	0.50	0.25

Table 3. Hay yields modelled and measured for first and second cuts at (a) St. Paulin in 2012 and 2013, and (b) St. Edouard in 2013 and 2014, and (a) above-ground tree biomass modelled and measured at St. Paulin before thinning in 2012.

(a) St. Paulin					
Variable	Year	TBI		mono	
		modelled	measured	modelled	measured
-----g C m ⁻² -----					
Yield 0-2 ^a	2012 1 st cut	31	132 ± 38		
Yield 2-6 ^b	2012 1 st cut	187	216 ± 42	185	229 ± 32
Yield 0-2 ^a	2012 2 nd	43	N/A		
Yield 2-6 ^b	2012 2 nd	133	N/A	136	N/A
Yield 0-2 ^a	2013 1 st cut	75	40 ± 26		
Yield 2-6 ^b	2013 1 st cut	177	172 ± 61	176	135 ± 43
Yield 0-2 ^a	2013 2 nd	56	N/A		
Yield 2-6 ^b	2013 2 nd	129	N/A	131	N/A
Tree biomass	2012 Sept.	902	689 ± 360		

(b) St. Edouard					
Variable	Year	TBI		mono	
		modelled	measured	modelled	measured
-----g C m ⁻² y ⁻¹ -----					
Yield 0-2 ^a	2013 1 st cut	23	45 ± 12		
Yield 2-5 ^b	2013 1 st cut	99	48 ± 9	97	72 ± 11
Yield 0-2 ^a	2013 2 nd cut	40	N/A		
Yield 2-5 ^b	2013 2 nd cut	103	N/A	101	N/A
Yield 0-2 ^a	2014 1 st cut	19	80 ± 19		
Yield 2-5 ^b	2014 1 st cut	78	92 ± 32	75	114 ± 26
Yield 0-2 ^a	2014 2 nd cut	48	49 ± 24		
Yield 2-5 ^b	2014 2 nd cut	111	67 ± 24	112	101 ± 27

^a measured values at 1 m from tree rows in 2013, 1.5 m from tree rows in 2012 and 2014

^b measured values at 6 m (SP) and 5 m (SE) from tree row in 2013, average of those at 3 and 6 m (SP) or 3 and 4.5 m (SE) from tree rows in 2012 and 2014.

Table 4. Modelled C budgets and N losses for zones of direct and indirect competition (0 – 2 and 2 – 6 m from trees; see text) in tree-based intercropping (TBI), and for monocropping (mono) during 2014 at St. Paulin.

Year		TBI				Mono	
		0 – 2 m		2 – 6 m		Total ^a	
		Poplar	Hard-wood	Clover/ Grass	Clover/ Grass	Clover/ Grass	
C Budget		-----g C m ⁻² y ⁻¹ -----					
GPP		861	216	586	1057	1259	1044
<i>R_a</i>	shoot	270	67	150	239	322	237
	root	111	33	152	279	284	277
	total	381	100	302	518	606	514
NPP	shoot	391	92	191	364	467	361
	root	89	24	93	175	185	169
	total	480	116	284	539	652	530
Litterfall	shoot	109	27	77	127	156	125
	Root ^b	55	18	89	176	171	174
	total	164	45	166	303	327	299
R_h			420		386	397	384
NEP			460		149	255	147
Harvest				99	218	178	218
NBP			361		-69	76	-72
		-----g N m ⁻² y ⁻¹ -----					
DIN loss			0.04		0.23	0.17	0.25

Note: Abbreviations: GPP: gross primary productivity, *R_a*: autotrophic respiration, NPP: net primary productivity, *R_h*: heterotrophic respiration, NEP: net ecosystem productivity, NBP: net biome productivity, DIN: dissolved inorganic N.

^a weighted for areas of 0 – 2 m and 2 – 6 m zones

^b includes exudation

Table 5. Modelled C budgets and N losses for zones of direct and indirect competition (0 – 2 and 2 – 5 m from trees; see text) in tree-based intercropping (TBI), and for monocropping (mono) during 2014 at St. Edouard.

Year		TBI				Mono	
		0 - 2		2 - 5		Total ^a	
		Poplar	Hard wood	Clover/ Grass	Clover/ Grass	Clover/ Grass	
C Budget		-----g C m ⁻² y ⁻¹ -----					
GPP		1042	22	474	993	1211	986
<i>R_a</i>	shoot	351	9	114	220	322	218
	root	143	3	113	246	251	245
	total	494	12	227	466	573	463
NPP	shoot	455	8	158	351	459	346
	root	93	2	89	176	179	177
	total	548	10	247	527	638	523
Litterfall	shoot	138	3	66	122	156	120
	root ^b	71	2	56	137	134	139
	total	209	5	122	259	290	259
R_h			324		291	304	290
NEP			477		237	334	233
Harvest				67	190	141	187
NBP			410		46	193	46
		-----g N m ⁻² y ⁻¹ -----					
DIN loss			0.04		0.82	0.52	0.87

Note: Abbreviations: GPP: gross primary productivity, *R_a*: autotrophic respiration, NPP: net primary productivity, *R_h*: heterotrophic respiration, NEP: net ecosystem productivity, NBP: net biome productivity, DIN: dissolved inorganic N.

^a weighted for areas of 0 – 2 and 2 – 5 m zones

^b includes exudation

Table 6. Total C exchange, changes in C stocks and N losses modelled from 1 January 2004 to 31 December 2014 at St. Paulin for tree-based intercropping (TBI) with trimming fractions of 0.33, 0.50 and 0.67 (see text), and for monocropping. All values are weighted for those in the 0 – 2 m and 2 – 6 m zones.

	TBI			Monocrop
Trimming Fraction	0.33	0.50	0.75	
C Exchange	----- g C m ⁻² 11 y ⁻¹ -----			
NPP	6979	6758	6429	5752
R _h	5294	5295	5300	5138
NEP	1685	1463	1129	614
Crop Harvest	1586	1690	1852	2088
Tree Removal ^a	676	564	357	0
DOC, DIC, CH ₄	4	5	5	5
Manure + Seeds	1560	1560	1560	1560
NBP	979	764	475	82
Change in C Stocks^b	----- g C m ⁻² 11 y ⁻¹ -----			
Tree AGB	726	517	308	0
Tree BGB	193	127	74	0
Crop AGB	2	3	4	3
Crop BGB	198	254	272	290
Δ SOC	-148	-147	-193	-216
Δ DIC	8	9	8	6
N Losses	----- g N m ⁻² 11 y ⁻¹ -----			
DIN	3.6	3.9	4.4	5.2

^a from tree thinning in 2012 (Table 1)

^b below-ground values are for the entire soil profile (0 – 1 m)

Table 7. Total C exchange, changes in C stocks and N losses modelled from 1 January 2004 to 31 December 2014 at St. Edouard for tree-based intercropping (TBI) with trimming fractions of 0.50, 0.67 and 0.83 (see text), and for monocropping. All values are weighted for those in the 0 – 2 m and 2 – 5 m zones.

	TBI			Monocrop
Trimming Fraction	0.50	0.67	0.83	
C Exchange	----- g C m ⁻² 11 y ⁻¹ -----			
NPP	4821	4483	4156	3724
R _h	3921	3894	3838	3721
NEP	900	690	318	3
Crop Harvest	849	918	1041	1073
Tree Removal	0	0	0	0
DOC, DIC, CH ₄	3	3	3	3
Manure + Seeds	350	350	350	350
NBP	398	119	-376	-723
Change in C Stocks^a	----- g C m ⁻² 11 y ⁻¹ -----			
Tree AGB	991	723	302	0
Tree BGB	215	153	68	0
Crop AGB	3	4	8	5
Crop BGB	166	222	254	285
Δ SOC	-983	-990	-1016	-1020
Δ DIC	6	7	8	7
N Losses	----- g N m ⁻² 11 y ⁻¹ -----			
DIN	5.0	5.1	6.1	7.7

^a below-ground values are for the entire soil profile (0 – 1 m)

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Fig 1: Hemispherical photograph taken midway between tree rows in the St. Edouard TBI treatment before being processed through GLA to determine sky fraction (see text).

Fig. 2. Schematic representation of TBI system modelled at St. Paulin (SP) and St. Edouard (SE), showing zones of direct (0 - 2 m from centre of tree row) and indirect (2 – 6 m (SP) or 2 – 5 m (SE) from centre of tree row) competition for light in 10 variably spaced canopy layers of equal LAI, and for water and nutrients in 8 fixed soil layers of increasing thickness.

Fig. 3: Root length density profiles modelled in the 0–2 m and 2–6 m zones of the TBI system at St. Paulin at the time of the first cut in July, 2011.

Fig. 4: *Ecosys* crop yields modelled at (a-c) St. Paulin and (d-f) St. Edouard for tree-based intercropping (TBI) with small (red symbols), intermediate (black symbols) or large (red symbols) tree trimming fractions (see text), and for monocropping (weighted average only).