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Title: Nutrient addition enhances carbon sequestration in soil but not plant biomass in a coastal shelter plantation in South China.

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Abstract:

Casuarina equisetifolia plantations have been widely established along tropical and subtropical coasts, where they act as a windbreak to shelter coastal areas. These shelter plantations also fulfill important ecosystem service by sequestering large amounts of carbon (C). However, shelter plantations are usually established on nutrient-poor sand dunes, which may limit tree growth and therefore C sequestration rates. To assess whether fertilization increases the C sequestration of coastal shelter plantations, we conducted a fertilization experiment in a young *C. equisetifolia* plantation with four treatments: nitrogen addition (+N), phosphorus addition (+P), nitrogen and phosphorus addition (+NP), and controls (CK). We quantified nutrient availability and annual net ecosystem production (NEP) during the key early establishment phase. Fertilization with +N and +P significantly increased ammonium-N and extractable P in the surface soils and the N and P concentrations of branches, respectively. Surprisingly, the mean growth rate of *C. equisetifolia* plantations (24.59 ± 0.66 Mg ha^{-1} yr^{-1}) was not affected by fertilization. The mean NEP was 6.18 ± 0.49 Mg C ha^{-1} yr^{-1}, and there was no difference among fertilization treatments. However, soil organic C significantly increased by 41% and 36% with +N and +P, respectively, but not +NP. *C. equisetifolia* plantations can sequester large amounts of C in biomass on poor soils without the need for additional nutrients, although fertilization may enhance soil C storage. Considering the potential large planting area, we suggest that coastal *C. equisetifolia* shelter plantations could be an important nature-based solution for climate change mitigation in coastal regions.

Keywords: windbreak, carbon sequestration, coastal protection, fertilization; shelter plantation.

1. Introduction

Sandy coasts, which dominate ocean shorelines globally, are more vulnerable to cyclones and climate change than other types of coasts (i.e. muddy and rocky coasts; Defeo et al., 2009). Over 70 % of sandy coasts have been eroded due to human activities and climate changes such as increased cyclone frequency and sea-level rise (Zhang et al., 2004). Shelter plantations can significantly mitigate the erosion of sandy coasts and protect the coastal area (Defeo et al., 2009; Sun et al., 2015), providing an efficient and economical alternative to coastal engineering on exposed sandy coasts (Kort et al., 1998). Wind-resistant tree species are planted in harsh environments and degraded ecosystems, like coastal sand dunes, to reduce wind damage and erosion (Srivastava, 1995; Tchichellea et al., 2017). However, shelter plantations also provide an important additional ecosystem service by sequestering large amounts of C in biomass and soils, which helps to mitigate climate change (Shan et al., 2018).

Globally, plantations are regarded as important C sinks and natural climate change solutions (Chen et al., 2011; Fang et al., 2001; Wu et al., 2014). For example, afforestation and reforestation in China alone increased national annual C sequestration from -0.010 Pg C in mid 1970s to 0.026 Pg C in late 1990s, most of which was attributed to the establishment of plantations (Fang et al., 2001). However, C sequestration by coastal shelter plantations has generally been neglected, and few studies have quantified their C sequestration potential (Wang et al., 2013); this is unsatisfactory because shelter plantations cover large areas (318 M ha), have high C accumulation rates (0.69 Mg C $ha^{-1}yr^{-1}$), and could therefore contribute substantially to global C sequestration (Bossio et al., 2020).

To protect China's coastal areas, since the 1950s, *Acacia*, *Eucalyptus*, *Pinus* and *Casuarina* species have been introduced into China's coastal regions to stabilize sandy beaches and reduce coastal erosion (Chen et al., 2017; Ge et al., 2019; Liu et al., 2011). In particular, over 300,000 ha of land have been planted with *Casuarina equisetifolia* L. (Zhong et al., 2010), a nitrogen-fixing species that is widely cultivated in tropical and subtropical regions (Gauthier et al., 1981). *C. equisetifolia* originates from Australia and Southeast Asia (Srivastava, 1995), and was introduced into China in 1897. Worldwide, around 8% of terrestrial land surface distributed in over 150 countries is suitable for planting *Casuarina* species (Potgieter et al., 2014) and *C. equisetifolia* is widely used for the stabilization and restoration of degraded lands because of its resistance to wind, drought and barren soils (Srivastava, 1995; Yang et al., 2007). Although *C. equisetifolia* is ideal for establishing plantations on barren sand dunes in coastal areas, severe soil nutrient deficiency still inhibits its growth and ecological function (Walker et al., 1993). Recent studies along a chronosequence of *C. equisetifolia* plantations showed that the gradual decline in soil nutrient availability over time results in negligible growth once the plantation is over 18 years of age (Wang et al., 2013; Xu et al., 2013). It is thus highly likely that the decline in soil nutrient availability eventually limits plant growth and leads to the degradation of *C. equisetifolia* shelter plantations (Xiao et al., 2007). However, the early development stage (3-10 years) of *C. equisetifolia* is the period of fastest biomass accumulation (Wang et al., 2013; Ye et al., 2008), resulting in particularly high demand of soil nitrogen (N) and phosphorus (P) in young plantations, which could determine overall C sequestration.

To maximize C sequestration in *C. equisetifolia* plantations, we need to understand how nutrient availability limits plant growth and ecosystem function, and assess whether fertilizer application will enhance biomass accumulation during the early stages of plantation establishment. To address this, we conducted a fertilization experiment in a three-year old *C. equisetifolia* shelter plantation on sandy soil to explore the effects of N and P addition on soil nutrient availability, plant growth rate, soil respiration and ecosystem C sequestration. The main objectives of this study were to detect the N and P fertilization effect on the C sequestration of *C. equisetifolia* plantations growing on sand dunes. We hypothesized that: 1) N and P addition would improve soil nutrient availability and enhance plant growth rates; 2) Greater enhancement of plant biomass than carbon turnover (soil respiration) by fertilization would result in net ecosystem C sequestration of the young *C. equisetifolia* shelter plantation.

2. Materials and Method:

2.1 Site description

The study site (111.01°E, 21.41°N) is located in Dianbai District, Maoming City, Guangdong Province, China, which has the earliest and most typical coastal *C. equisetifolia* shelterbelt (over 100 km long and average 100 m width along the coastline, Fig. 1). The landform is typical of sandy coasts in South China, and the climate is tropical monsoon, with a rainy season from April to September and a dry season from October to March. During the study period from October 2012 to September 2013, the precipitation during the rainy and dry seasons was 1524 mm and 402 mm, respectively. The annual mean temperature is 23 ℃, with the highest mean temperature (30 ℃) in July and lowest mean temperature (18 ℃) in January. The soil is coastal aeolian sand, with 92% sand, 4% silt and 4% clay and a pH of 7.6. *C. equisetifolia* was first introduced to the study region in the early 1960s but the shelter plantations are frequently destroyed by typhoons, and reforestation (with the same species) generally occurs immediately after clear-cutting the destroyed trees.

2.2 Experimental Design

The experiment was conducted in a three-year old plantation, which was reforested in March 2009 at a planting density of 2500 trees ha^{-1} after clear-cut of an old plantation that was destroyed by a typhoon. We established 20 plots measuring 10 m × 10 m each in a completely randomized design, with five replicates of four treatments: N addition (+N), P addition (+P), N and P addition (+NP) and a control treatment (CK) with no nutrient addition. From Oct. 2011 to Apr. 2013, nitrogen was applied every six months as 536 g uncoated urea ($CO(NH_2)_2$), which was equal to 250 g N per plot, and P was applied every six months as 1387 g dicalcium phosphate ($CaHPO_4 \cdot 2H_2O$), equal to 250 g P per plot. Total fertilization rates where therefore 50 kg (N or P) ha^{-1} yr^{-1}. The fertilizers were applied as evenly as possible by hand, at least one meter away from each sapling, and covered by sand.

2.3 Soil sampling and analysis

Soils samples were taken from 0-20 cm depth at five random locations within the plantation before fertilization in Oct. 2011 and at five random locations within every plot in Oct. 2013, after two years of fertilization and six months after the last fertilizer application. Soil samples were collected using a 5-cm diameter soil corer and split into two depth increments of 0-10 cm and 10-20 cm for analysis.

Gravimetric soil water content (SWC) was measured by oven-drying for 24 h at 105 °C. Soil organic carbon (SOC) content was determined with the high-temperature external thermal oxidation-ferrous iron titration method (Walkley & Black, 1934). Soil TN and TP were digested with micro-Kjeldahl digestion and determined by a flow injection autoanalyzer (FIA, Lachat Instruments, USA). Soil NH_4-N and NO_3-N were extracted from 8 g fresh soil in 40 ml 2 M KCl solution and determined by a flow injection autoanalyzer (FIA, Lachat Instruments, USA). Soil available phosphorus (AP) was extracted from 8 g air-dried soil in 40 ml Bray-2 solution and measured with the acid-soluble molybdenum-antimony colorimetric method (Liu et al., 1996). The basic characteristics of the unfertilized soil are listed in Table S1.

2.4 Biomass measurements

The height (H) and diameter at breast height (DBH) of all trees in the plots were recorded each year in October from 2011-2013. To calculate the standing biomass of roots, stems, branches and branchlets, we used a growth model (Table S2) that was specifically developed for *C. equisetifolia* in Southern China (Hong et al., 2010). Monthly litter removal is a common management practice to reduce fire risk in *C. equisetifolia* plantations and we therefore estimated litter production from the standing biomass. As *C. equisetifolia* plantations of different ages have similar ratios of litter production and standing biomass (Table S3) we applied a correction factor derived from young (six year-old) *C. equisetifolia* plantations (Ye et al., 2008):

$$L = B \times LB \qquad \text{(E1)}$$

Where L is litter production, expressed as Mg C ha^{-1} yr^{-1}, B is total standing biomass expressed as Mg C ha^{-1}, and LB is the ratio of litter production to biomass.

Plant samples for analysis of nutrient concentrations were collected before fertilization in October 2011 and at the end of the study in October 2013. We selected five healthy plants in each plot and collected four branches from each plant (one from each cardinal point). The initial N and P concentrations of stems, branches and branchlets (functional leaf of *C. equisetifolia*) are listed in Table S4. Branchlets and branches of *C. equisetifolia* were ground and digested with concentrated sulfuric acid. Nitrogen concentrations were measured by indophenol blue colorimetry (Ivančič & Degobbis, 1984), and P concentrations were measured by molybdenum-antimony colorimetry (Liu et al., 1996).

2.5 Soil CO_2 efflux measurement

We partitioned total soil CO_2 efflux (R_s) into heterotrophic respiration (R_h) and autotrophic respiration (R_a) by trenching. A pair of adjacent PVC (20 cm internal diameter, 5 cm height) collars were inserted 3 cm into the soil and 0.5 m apart in every plot; roots were excluded from one collar by inserting four 0.5-m ×1-m PVC plates into the soil to 1-m depth in May 2012. The trenched collar was used to measure R_h, and the untrenched collar provided measurements of R_s, which were then used to estimate R_a according to Edwards and Harris (1977):

$$R_s = R_h + R_a \tag{E2}$$

Soil CO_2 efflux, temperature and moisture were measured monthly with an automated soil CO_2 flux system (LI-8100; LI-COR Biosciences, Lincoln, NE, USA) from May 2012 to September 2013. As measurements conducted at 9:00 am are close to the daily means in the area (Tang et al., 2006), our measurements between 9:00 and 11:00 am are representative of daily mean values. To limit the influence of root decomposition on measurements of R_h, we excluded the first five months of data after trenching. To estimate annual CO_2-C released by each component of soil respiration, we multiplied the monthly mean values by the number of days in each month and then summed the monthly totals for October 2012 to September 2013 to give annual values of R_s, R_a, and R_h in Mg C ha^{-1} yr^{-1}.

2.6 Estimates of total C sequestration

We estimated net primary production and net ecosystem production in the *C. equisetifolia* plantation without rhizodeposition and fine root turnover (*NPP* and *NEP, respectively*) using simplified equations (Gower et al., 2001):

$$NPP = \Delta B + L \tag{E3}$$

Where ΔB is the annual increment of biomass and L is annual litter production as a proportion of living biomass (Ye et al., 2008). We then estimated annual *NEP* from *NPP* and R_h:

$$NEP = NPP - R_h \tag{E4}$$

Hence, *NEP* includes root respiration but as *NPP* and *NEP* do not include rhizodeposition and root turnover, the values are lower than total NPP and NEP.

2.7 Statistical analysis

We assessed the individual or interactive effects of N fertilization and P fertilization on soil properties, plant biomass, N and P concentrations of plant tissues, *NPP* and *NEP* using two-way analysis of variance (ANOVA); when the results were significant, we evaluated individual treatment differences by Turkey HSD post-hoc tests. Monthly soil respiration was analyzed by repeated measures two-way ANOVAs. The data normality was checked with Levene's test before the analysis, and all the data were homogeneous. The statistical analyses were performed with SPSS 20.0 for Windows (SPSS Inc., Chicago, USA) and figures were created with Origin Pro 9.0 (OriginLab Corp., Northampton, USA). Results are reported as significant at $P<0.05$.

3. Results

3.1 Soil characteristics and respiration rates

Before fertilization in 2011, soil nutrient concentrations did not differ between soil depth increments (Table S1), but after two years of fertilization in 2013, soil nutrient concentrations tended to be higher in the surface layer (0-10 cm depth; Table 1). Compared with CK plots, +P fertilization increased soil AP concentration 2.8-fold ($P=0.024$) at 0-10 cm depth, but there was no effect of +NP fertilization on AP. Soil organic C content at 0-10 cm depth increased by 41% and 36% with +N and +P, respectively, but not with +NP fertilization (Table 1). Fertilization had no effect on any soil characteristics at 10-20 cm depth.

Fertilization did not affect total soil respiration or its heterotrophic and autotrophic components throughout the year (Table 2 & Fig. 2). Across all treatments, R_h contributed 74-79%, whereas R_a only contributed 21-26% to R_s. Both R_s and R_a *were* positively associated with soil temperature ($P<0.01$ for both, Fig. 3)

3.2 Plant growth rate and ecosystem productivity

Surprisingly, fertilization with +N and +P did not affect plant growth rate. From 2011 to 2013, the biomass accumulation of *C. equisetifolia* increased from 22.83 ± 1.37 Mg ha^{-1} to 64.32 ± 1.75 Mg ha^{-1} (Fig. 4), but total biomass accumulation and estimated litter production did not differ among treatments (Table 2). Neither N nor P fertilization affected the *NPP* or *NEP* of the plantation (Table 2).

Although the N and P concentrations of branches increased with +N and +P fertilization, respectively (Fig. 5d & 5e), the N and P concentration of branchlets did not (Fig. 5), and there was no effect of +NP addition on nutrient concentrations in plant tissues.

4. Discussion

4.1 The effects of fertilization on soil and plant characteristics

Despite growing on nutrient-poor sandy soils, we found surprisingly little effect of fertilization on plant and soil during the establishment of the *C. equisetifolia* plantation (Table 1&2). Plant growth in tropical and subtropical forests is mainly limited by P availability (Li et al., 2017; Mo et al., 2015), because P limitation usually occurs on strongly weathered soils (Vitousek, 1984; Vitousek & Sanford, 1986). However, coastal sandy soils have undergone a much shorter period of soil development and are thus usually regarded as N deficient (Hayes et al., 2014; Hobbie & Vitousek, 2000). The coastal sandy soils in our study had total only *c.* 5 % of the total N and 25.5 % of the total P concentrations of inland soils in the region (Li et al., 2014). We therefore expected that the plants in our sandy dunes would face severe N limitation rather than P limitation, and we thus hypothesized that extra inputs of N should benefit the ecosystem. Although previous fertilization experiments found that N addition promoted the growth of N-limited temperate and boreal forests (Li et al., 2017; Yang et al., 2014), in our study, the effects of N fertilization were very limited, and we observed no effect of N-fertilization on plant growth.

Based on plant biomass production and the nutrient concentration in plant tissues (Figure 4&5), we estimated that the annual N requirement of the vegetation in the CK plots was *c*. 69% higher than the amount of N added as fertilizer (Table S5), which suggests that the trees have access to other sources of N. One potential source of N is biological fixation via symbiotic actinobacteria, which explains the persistence of *C. equisetifolia* on low N soils (Gauthier et al., 1981). Previous studies had shown that *C. equisetifolia* can obtain 38-67% of the N required for growth from N fixation (Mariotti et al., 1992; Parrotta et al., 1994). The second potential source of N is through atmospheric deposition, as wet deposition in the study area is *c*. 40 kg N ha^{-1} yr^{-1} (Mo et al 2015). Hence, biological N fixation combined with high rates of atmospheric N deposition could meet much of the N demand of young *C. equisetifolia* plantations, which might explain why the addition of N had no effect on the growth of *C.*

equisetifolia despite the poor sandy soil. Indeed, higher concentrations of soil NH_4-N at 0-10 cm depth and N in branches indicate that N is unlikely to be limiting to *C. equisetifolia* plantations in the study area.

Although we expected primary limitation by N, the substantial decline in total soil P after two years' growth indicates a high demand for P in the plantation (Table 1). Moreover, the available P concentration in CK plots was only 0.04 mg kg^{-1}, which is much lower than a nearby tropical forest, which is regarded as P-limited (Mo et al., 2019; Monaco & Prouzet, 2015; Wang et al., 2014). Despite low concentrations of available P, fertilization with P also had minor effects and did not increase plant growth. It is possible that *C. equisetifolia* is not strongly limited by P because it can form symbiotic associations with both ecto- and endomycorrhizal fungi (Diagne et al., 2013). Several studies have shown that growth and N and P accumulation in *C. equisetifolia* seedlings are enhanced significantly by inoculation with effective symbionts (Muthukumar & Udaiyan, 2010; Sempavalan et al., 1995; Vasanthakrishna & Bagyaraj, 1993; Ye, 1996). The low estimated P uptake by *C. equisetifolia*, increased availability of soil P with fertilization, and the storage of additional P in woody tissues (branches) indicate that P supply exceeded demand (Table S5), suggesting that P was not limiting to plantation growth in our study area.

Another possible explanation for the minor effect of fertilization on plant growth is the inputs of sea spray aerosol particles (SSA) formed through wave breaking (Bertram et al., 2018). SSA contains substantial amounts of Na^+, Ca^{2+} and other elements that may benefit the growth of plants (Starinsky et al., 1983). Furthermore, polluted SSA enriched in ammonium-N and nitrate-N (Bertram et al., 2018; Vet et al., 2014) can directly reach the canopy of *C. equisetifolia* planted in coastal areas. Therefore, it is possible that nutrient inputs by SSA might obscure or reduce the effect of fertilization on plant biomass in our study. We also found no effect of fertilization on soil CO_2 efflux, which seems surprising, as many previous studies have demonstrated positive (Xiao et al., 2020) or negative (Janssens et al., 2010) effects of N addition on soil respiration, and greater mineralization of soil C with P enrichment (Bradford et al., 2008; Hobbie & Vitousek, 2000). Whereas the lack of fertilization effects on plant growth rate and plant biomass may explain why R_a remained unchanged with N- and P-addition, the lack of a response for R_h might be due to the low C content of the sandy soil, which could constrain microbial activity (Su et al., 2016). In addition, whereas R_h generally makes a large contribution to total soil respiration, R_h is likely to be strongly reduced by the regular removal of litter (Sayer & Tanner, 2010) as a management practice in *C. equisetifolia* plantations.

Although fertilization did not influence plant biomass or soil respiration (Fig. 2&4), SOC in the topsoil increased substantially with both +N and +P. The storage of SOC is determined by the balance between inputs of C in organic material such as plant litter and root products, and losses of C through heterotrophic respiration (Post et al., 1982). As litterfall, one of main inputs of organic matter, was removed to control fires, we propose that increased SOC in the topsoil could be due to enhanced fine root turnover and changes in root distribution, which we did not measure. Fertilization in terrestrial ecosystems can increase the fine root turnover in poor soils (Yuan & Chen, 2012), especially in the topsoil (Ferreira et al., 2018; Wang et al., 2019) and a recent study in *C. equisetifolia* plantation also found that soil N availability was positively correlated with fine root biomass (Hu et al., 2017). In our study, changes in root turnover and distribution, rather than biomass, could enhance soil C inputs without a significant increase in R_a. We thus speculate that fertilization altered fine root distribution, leading to a greater concentration of fine roots in surface soils, and greater fine root turnover increased C inputs to the soil (Fig. 6).

4.2 Carbon sequestration potential of *C. equisetifolia* plantations

The biomass of *C. equisetifolia* increased three-fold between 2011 and 2013, with an average growth rate of 24.59 ± 0.66 Mg ha^{-1} yr^{-1} and mean *NEP* was 6.18 ± 0.49 Mg C ha^{-1} yr^{-1} (Table 2), which is higher than mean *NEP* (4.00 Mg C ha^{-1} yr^{-1}) estimated for tropical and subtropical afforestation worldwide (Chen et al., 2019). A field study demonstrated that afforestation of pasture in tropical regions increased annual NEP up to 4.42 Mg C ha^{-1} yr^{-1}, which transformed the land from a C source to a C sink (Wolf et al., 2011). The establishment of *C. equisetifolia* shelter plantations on sandy coasts thus provide substantial benefits in terms of C sequestration, besides their function as a windbreak. Plantations of *C. equisetifolia* in particular might be advantageous for C sequestration on sandy coasts compared with plantations of other species (Wang et al., 2013; Ye et al., 2008). For example, studies in a nine-year old shelterbelt forest in Fujian, China, showed that *Casuarina* plantations sequestered more C than *Acacia* and *Eucalyptus* plantations (Ge et al., 2019; Ge et al., 2018). Similarly, Yang and Guan (2006) found that *C. equisetifolia* plantations have higher annual production (14.51 Mg ha^{-1} yr^{-1}) than other plantations in the Pearl River Delta, China. Indeed, despite the low potential productivity of ecosystems on such sandy, nutrient-poor soils, coastal *C. equisetifolia* plantations have surprisingly high C sequestration rates, even compared to some inland plantations on much richer soils. Indeed, the *NEP* of our *C. equisetifolia* plantation is higher than the *NEP* of plantations of the N-fixing *Acacia crassicapa* (3.33 ± 0.76 Mg C ha^{-1} yr^{-1}; Chen et al. 2011) as well as the *NEP* reported for spruce stands (3.41±1.2 Mg C ha^{-1} yr^{-1}), broadleaf forests (2.19±1.11 Mg C ha^{-1} yr^{-1}), tropical plantations (4.68±1.30 Mg C ha^{-1} ha^{-1}), temperate plantations (3.14±0.78 Mg C ha^{-1} yr^{-1}) and even some tropical rainforests (1.19 Mg C ha^{-1} yr^{-1}; Chen et al., 2019; Tan et al., 2010).

4.3 Implications for forest management

Our study demonstrates that shelter plantations of *C. equisetifolia* represent a significant C sink in the early stage of growth, even without nutrient addition. Their benefits in terms of C sequestration are particularly important for coastline forest management in tropical China, as they are the only species which grow well in the nutrient-poor sand dunes. Based on our estimates of C sequestration for the plantation in the study area, afforestation with *C. equisetifolia* shelter plantations at the national level would provide C sequestration benefits of over 9.8×10^{5} Mg C yr^{-1} without the need for fertilizer applications, which reduces the cost of forest management. However, we note that the low biodiversity in monoculture *C. equisetifolia* plantations could compromise the stability of the ecosystem and threaten their potential to sequester C over longer time scales.

5. Conclusions

Our results show that young *C. equisetifolia* shelter plantations (3-5 years old) in regions characterized by high N deposition accumulate large amounts of biomass C without the need for fertilization, although nutrient addition may enhance soil C storage. Hence, shelter plantations can play an important role both as windbreak and C sinks, especially as the C sequestration capacity of *C. equisetifolia* plantations during the early establishment stage is higher than many other forest ecosystems. Although we demonstrate that the nutrient requirements of young *C. equisetifolia* plantations can be met without the need for fertilization, our study only considered N and P, which does not rule out limitation by other nutrient elements. We suggest that afforestation with *C. equisetifolia* could be an important climate change mitigation measure for coastal regions. To maximize the ecosystem services provided by *C. equisetifolia* plantations, future studies should assess the mechanisms underpinning soil C storage in shelterbelt plantations, as well as the role of other nutrients, especially during the longer-term development of *C. equisetifolia* plantations.

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Author Contributions

FMW and ZAL conceived and designed the study. FMW, XX, QFM, YWL, YXL, BZ carried out the experiment. YXF and FMW analyzed the data and wrote the first draft of the manuscript. All authors contributed to the interpretation of results and revising the manuscript.

Data availability

All the raw data related to this study will be made publicly available upon publication.

Conflict of Interests

The authors declared no conflicting interests.

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Tables:

Table 1. Soil physical and chemical characteristics at two depth increments in a tropical *C. equisetifolia* plantation after two years of fertilization, where CK is unfertilized controls, +N is nitrogen addition, +P is phosphorus addition, and +NP is nitrogen and phosphorus co-addition. TN is total nitrogen (N), NH_4-N is ammonium-N, NO_3-N is nitrate-N, TP is total phosphorus (P), AP is available P, N/P is the ratio of N to P; SOC is soil organic carbon (C), C/N is the C to N ratio and SWC is soil water content. Mean values ±S.E. are given for $n = 5$ plots per treatment and different superscript letters within a row denote differences among treatments at $P < 0.05$. Different letters above columns indicate differences among treatments at $P<0.05$, determined by post-hoc tests.

Soil Layers	**Treatment**	**TN ($g\ kg^{-1}$)**	**NH_4-N ($mg\ kg^{-1}$)**	**NO_3-N ($mg\ kg^{-1}$)**	**TP ($g\ kg^{-1}$)**	**AP ($mg\ kg^{-1}$)**	**N/P**	**SOC ($Mg\ ha^{-1}$)**	**C/N**	**SWC (%)**
0-10 cm	**CK**	0.14±0.004	1.01±0.08	0.52±0.38	0.10±0.01	0.05±0.003^{b}	1.38±0.12	4.33±0.33^{b}	21.27±2.20	0.30±0.12
	+N	0.17±0.02	1.57±0.15	2.03±0.71	0.11±0.02	0.06±0.01^{b}	1.60±0.23	6.11±0.58^{a}	24.38±0.93	0.12±0.02
	+P	0.15±0.02	1.21±0.20	2.05±0.75	0.14±0.03	0.19±0.07^{a}	1.14±0.13	5.90±0.33^{ab}	28.82±3.87	0.14±0.01
	+NP	0.14±0.02	1.11±0.17	1.03±0.28	0.14±0.02	0.08±0.01^{ab}	1.20±0.32	5.05±0.48^{a}	26.19±3.48	0.13±0.01
10-20 cm	**CK**	0.09±0.01	0.89±0.07	-	0.07±0.004	0.02±0.01	1.26±0.16	4.22±0.78	30.85±2.99	0.48±0.14
	+N	0.10±0.01	1.14±0.35	-	0.08±.01	0.04±0.02	1.35±020	4.16±0.31	29.23±3.68	0.57±0.11
	+P	0.09±0.01	0.87±0.12	-	0.11±0.04	0.41±0.37	1.09±0.27	3.67±0.34	28.08±3.75	0.51±0.09
	+NP	0.09±0.01	0.77±0.09	-	0.10±0.02	0.06±0.02	0.94±0.13	3.33±0.32	26.41±3.41	0.55±0.09

Note: "-" indicates concentration of NO_3-N below detection limits.

Table 2. Total soil respiration (R_s), root respiration (R_a) and heterotrophic respiration (R_h), biomass increment (ΔB), litter production (L), net primary production (*NPP*) and net ecosystem production (*NEP*) in a young *C. equisetifolia* plantation during a two-year fertilization experiment; CK is unfertilized controls, +N is nitrogen addition, +P is phosphorus addition, and +NP is nitrogen and phosphorus co-addition; annual mean values ±S.E. are given for $n = 5$ plots per treatment as Mg C ha^{-1} yr^{-1} based on measurements made from October to September in each year).

	R_s	R_a	R_h	ΔB		L		*NPP*		*NEP*
	2012-2013	2012-2013	2012-2013	2011-2012	2012-2013	2011-2012	2012-2013	2011-2012	2012-2013	2012-2013
CK	7.16±0.62	1.48±0.07	5.68±0.65	10.72±0.72	12.53±0.85	0.33±0.02	0.55±0.02	11.05±0.72	13.09±0.87	6.66±1.11
+N	8.20±0.21	1.95±0.31	6.25±0.23	10.68±0.87	10.66±0.65	0.34±0.02	0.54±0.03	11.02±0.87	11.19±0.67	5.43±0.57
+P	8.28±0.48	1.89±0.24	6.39±0.46	13.53±1.05	11.11±0.80	0.38±0.03	0.60±0.03	13.91±1.05	11.70±0.78	5.48±1.45
+NP	7.58±0.49	2.01±0.29	5.58±0.46	11.29±0.81	12.04±0.54	0.36±0.04	0.59±0.02	11.66±0.83	12.62±0.85	7.11±0.92

Fig. 1. The Casuarina equisetifolia shelterbelt plantation in Bohe Town, Dianbai District, Maoming City, Guangdong, China (111.12°E, 21.45°N) in May 2017; photo courtesy of the Forestry Bureau of Dianbai District.

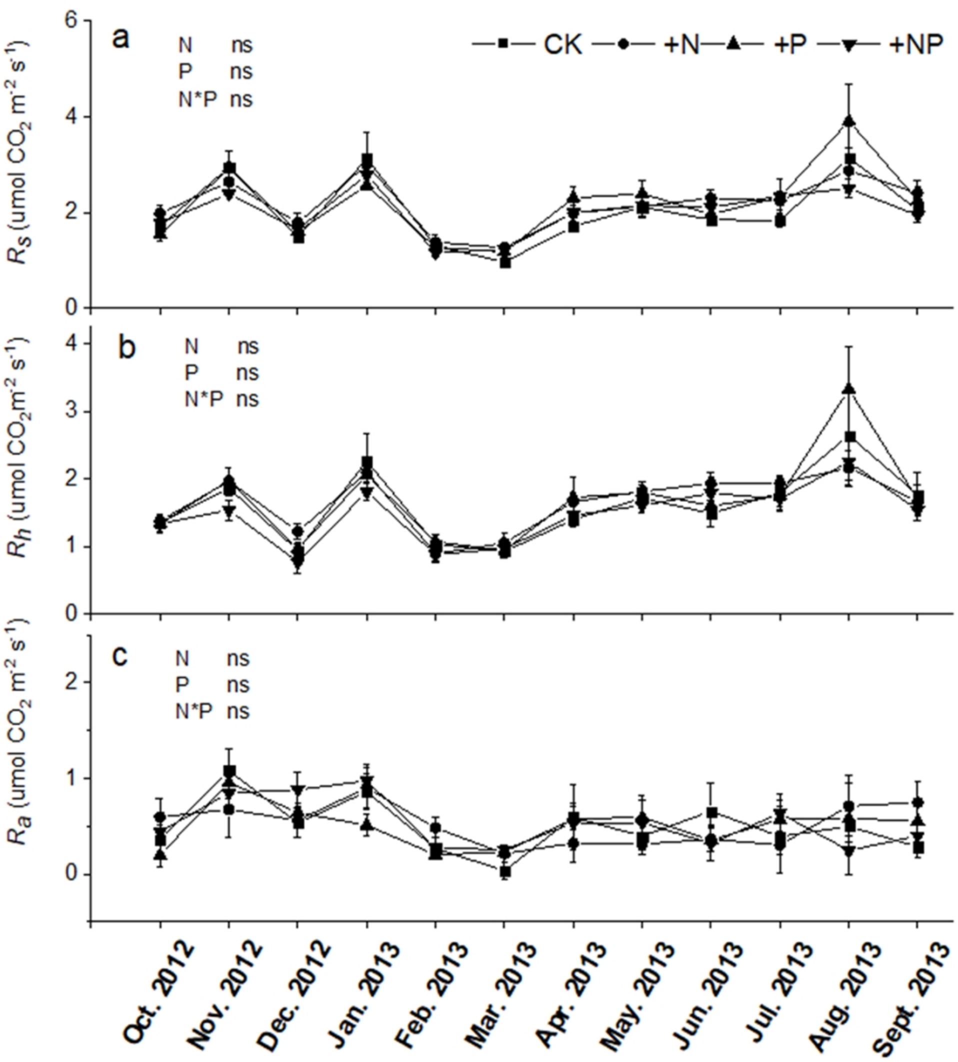

Fig. 2. Soil CO2 efflux partitioned into a) total soil respiration (Rs); b) heterotrophic respiration (Rh) and c) autotrophic respiration (Ra) in a C. equisetifolia plantation measured from October 2012 to September 2013 during a two-year fertilization experiment, where CK is unfertilized controls, +N is nitrogen addition, +P is phosphorus addition, and +NP is nitrogen and phosphorus co-addition; mean values ±S.E. are given for n = 5 plots per treatment; the significance of terms from repeated-measures two-way ANOVAs are shown, where ns is not significant at P < 0.05.

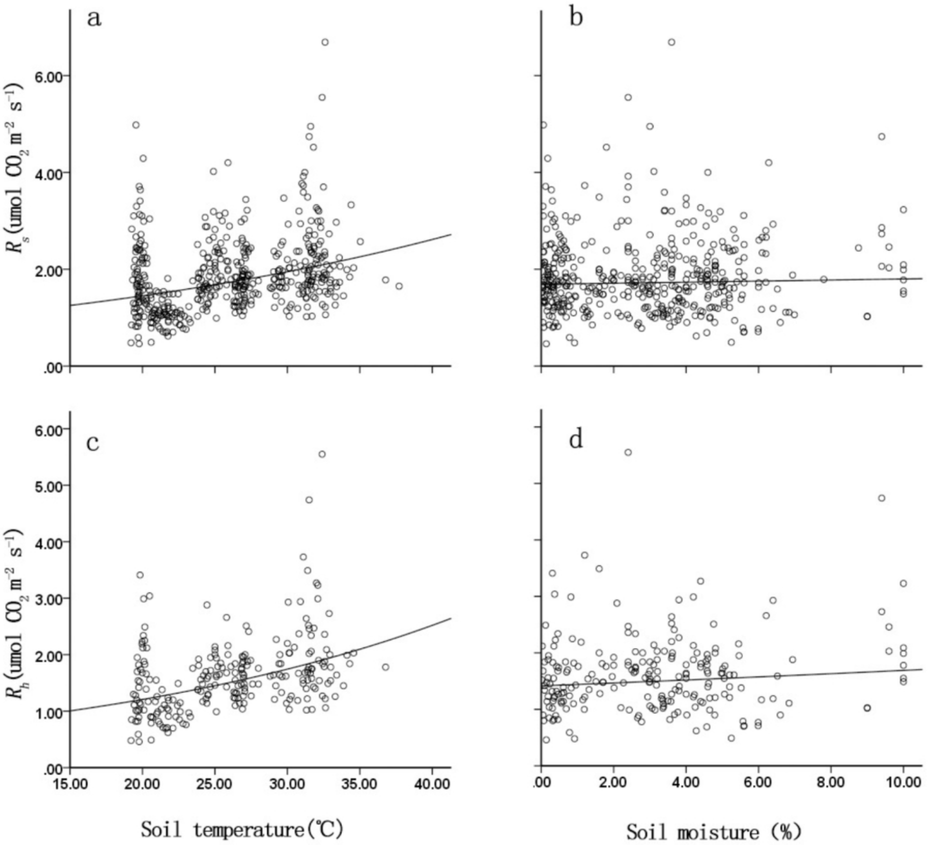

Fig. 3 The relationships between the components of soil respiration and soil temperature or water content in C. equisetifolia plantation from Oct. 2012 to Sept. 2013, showing exponential regressions of a) Total soil respiration (Rs) and soil temperature (R2=0.087, P<0.01). b) Rs and soil moisture (R2=0.01, P=0.46); c) Heterotrophic respiration (Rh) and soil temperature (R2=0.188, P<0.01); d) Rh and soil moisture (R2=0.011, P=0.11).

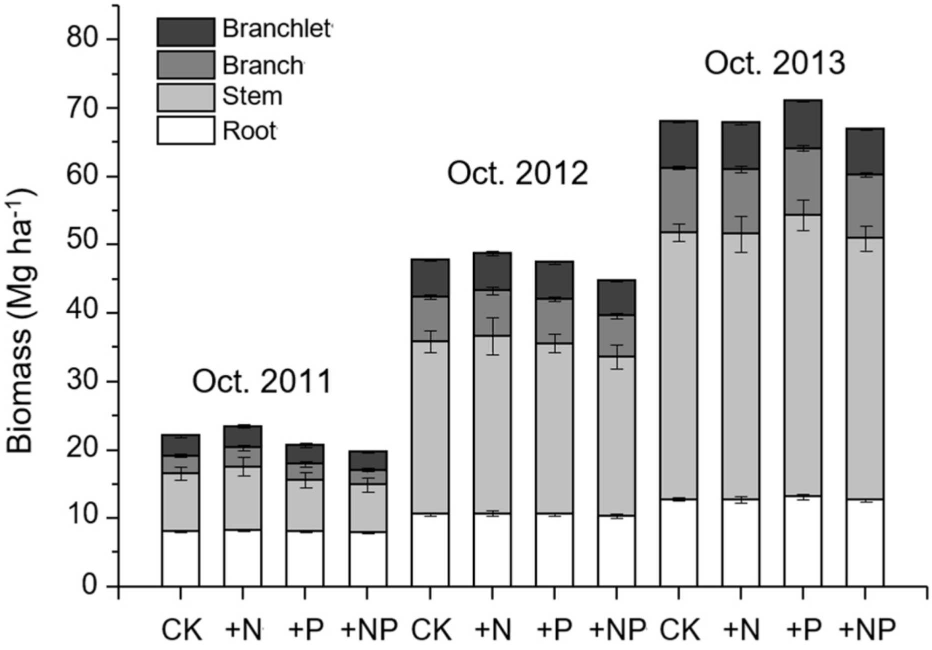

Fig. 4. Total dry mass of C. equisetifolia tissues from October 2011 to October 2013, where CK is unfertilized controls, +N is nitrogen addition, +P is phosphorus addition, and +NP is nitrogen and phosphorus co-addition; mean values ±S.E. are given for n = 5 plots per treatment.

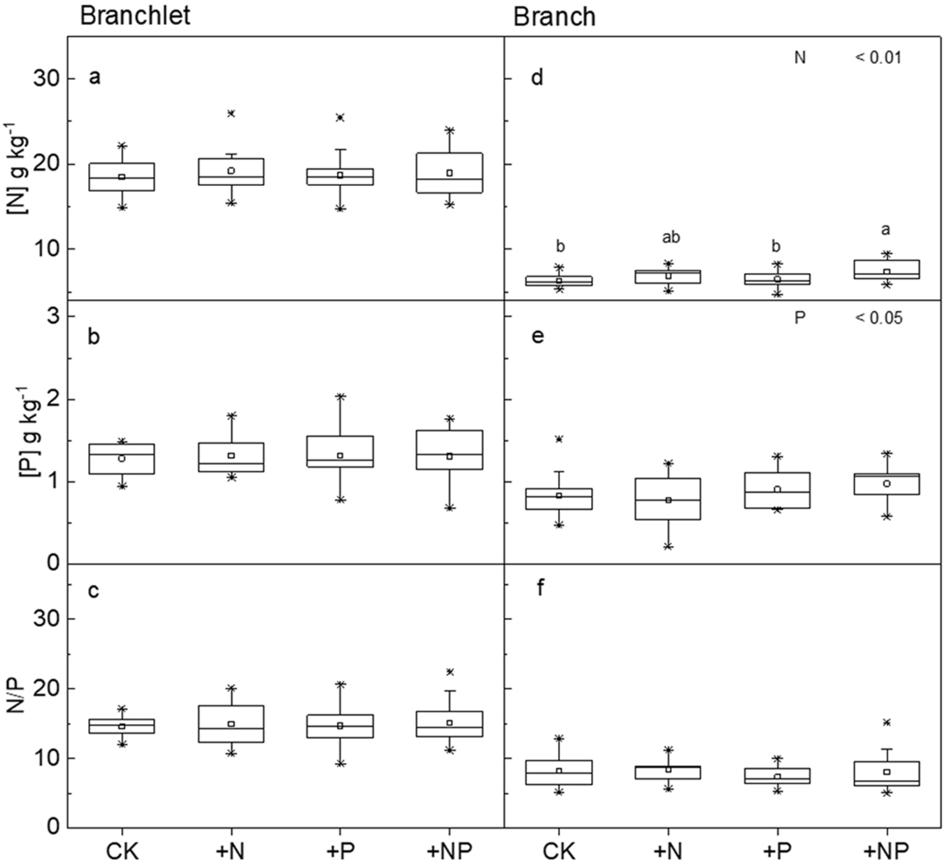

Fig. 5. Nutrient concentrations in branchlets (a-c) and branches (d-f) of C. equisetifolia collected from a young plantation after two years of fertilization in October 2013, showing nitrogen concentrations [N] (a, d), phosphorus concentrations [P] (b, e) and the N/P ratio (c, f); CK is unfertilized controls, +N is nitrogen addition, +P is phosphorus addition, and +NP is nitrogen and phosphorus co-addition; mean values ± S.E. are given for n = 5 plots per treatment; the significance of terms from two-way ANOVAs are shown at $P < 0.05$ or $P < 0.01$; and different letters above boxes indicate differences among treatments at $P < 0.05$, determined by Tukey post-hoc tests.

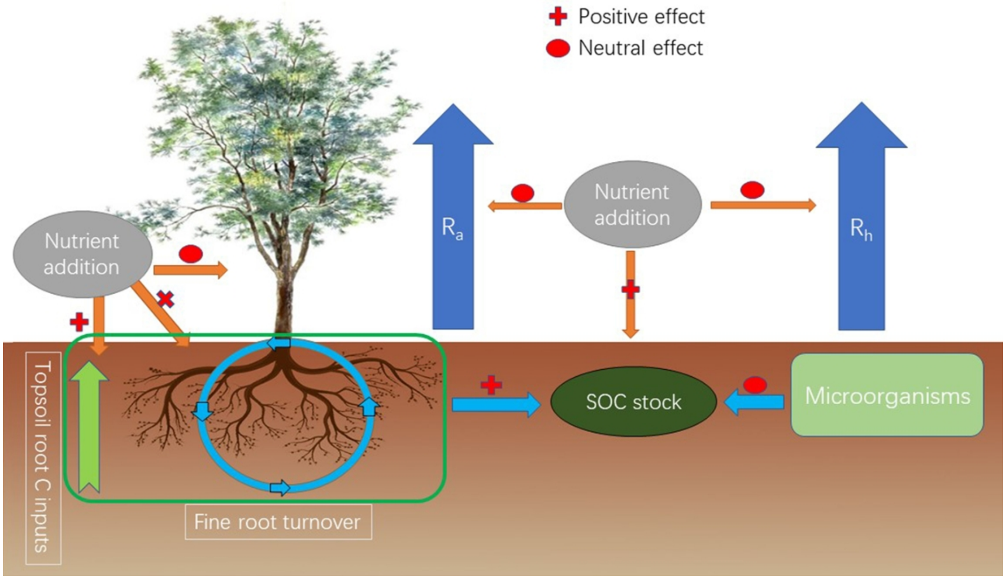

Fig. 6. A mechanistic framework to explain how fertilization might enhance soil organic carbon (SOC) sequestration without increasing aboveground biomass in C. equisetifolia shelter plantations; whereby nutrient addition alters the balance between carbon inputs and outputs by enhancing fine root turnover, which increases topsoil carbon (C) inputs, but without stimulating aboveground biomass growth, autotrophic respiration (Ra), or heterotrophic respiration (Rh).