Carbon Stocks and Dynamics in Miombo, *Pinus* and *Eucalyptus* Forests in Mozambique

Assessment Tools and Tree Species Effects

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Cover: Illustration of (left foreground) a mountain miombo forest in the Western highlands of Manica province (left), located adjacent to (right) an approximately 34-year-old plantation of *Pinus taeda* (Photo: Bengt Olsson).

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Abstract

In Mozambique and neighbouring countries, deforestation and degradation of miombo forests are counteracted by new plantations of fast growing species and conservation of natural woodlands, activities supported by the REDD+ mechanism. The aim of this thesis was to examine the impacts of plantations of *Pinus* and *Eucalyptus* compared with *mountain* miombo forest on carbon stocks and dynamics in soil and tree biomass. The thesis also aimed to develop allometric biomass equations for *lowland* miombo forest to estimate aboveground tree biomass at the landscape scale. The entire study area was located within the Beira development corridor region, central Mozambique. Study plots of *mountain* miombo and 34-year-old first rotation plantations of *Pinus taeda* and *Eucalyptus grandis* were selected on three study sites in the Western highland of the Manica province to investigate total ecosystem carbon and nitrogen stocks in soil, litter and biomass. Tree biomass was estimated using allometric equations found in the literature. Total ecosystem carbon stocks in soils, litter layer and biomass, and net ecosystem production were all significantly higher in *P. taeda* and *E. grandis* plantations than in adjacent *mountain* miombo forest. Net primary production were higher in *P. taeda* and *E. cloeziana* plantations than in adjacent *mountain* miombo forest. Total soil nitrogen stocks in the topsoil layers were also significantly higher in plantation stands. The higher soil stocks of carbon and nitrogen could be explained to some extent with higher leaf litterfall, from Q-model predictions. However, higher root litter production in plantation stands was probably an additional important contribution to the measured higher soil organic carbon stocks. Two biomass functions were developed for estimating aboveground tree biomass of mixed-species *lowland* miombo forest. One equation was developed for estimating biomass based on stem diameter at breast height (1.3 m). The other equation was developed for estimating biomass based on stem diameter at stump height, to make it possible to also estimate losses of biomass in high exploitation areas of miombo woodlands.

Keywords: Biomass equation, *Brachystegia spiciformis, Eucalyptus grandis Eucalyptus cloeziana, Pinus taeda,* Fine root production, Litterfall, Net primary production, Soil carbon.

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Dedication

To my wonderful wife and daughters.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I **Guedes, B.S.**, B.A. Olsson and E. Karltun. (2016). Effects of 34-year-old *Pinus taeda* and *Eucalyptus grandis* plantations on soil carbon and nutrient status in former *miombo* forest soils. *Global Ecology and Conservation* 8, 190-202.

II **Guedes, B.S.**, B.A. Olsson, E. Karltun, A.A. Sitoe and G. Egnell. Impacts of 34-year-old plantations of *Pinus taeda* and *Eucalyptus grandis* on total carbon stocks in former miombo woodlands (Submitted).

III **Guedes, B.S.**, B.A. Olsson, A.A. Sitoe and G. Egnell. Net primary production and carbon fluxes in plantations of *Pinus taeda* and *Eucalyptus cloeziana* compared with miombo woodlands in Mozambique (Submitted).

IV Olsson, B.A., **B.S. Guedes**, S. Dahlin and R. Hyvönen. Predicted long-term effects of decomposition of leaf litter from *Pinus taeda*, *Eucalyptus cloeziana* and deciduous miombo trees on soil (Submitted).

V **Guedes, B.S.**, A.A. Sitoe, and B.A. Olsson. Allometric models to support landscape management of lowland miombo woodlands in Mozambique (Submitted).

Paper I is reproduced with permission of the publisher.

The contribution of Benard Guedes to the papers included in this thesis was as follows:

I, II and III	Planned and designed the studies together with co-authors. Performed field and laboratory work. Analysing and interpretation of the results together with co-authors. First author.
IV	Planned and designed the study together with co-authors. Performed field and laboratory work. Conducted data analyses, apart from Q-model work, and interpretation of the results together with co-authors. Co-author.
V	Planned, designed and performed field and laboratory work together with A. Sitoe. Analysing and interpretation of the results together with co-authors. First author.

Abbreviations

CEAGRE	Center for Agriculture and Natural Resource Studies, Faculty of Agronomy and Forestry Engineering
DNTF	National Directorate of Land and Forests
IIAM	Agricultural Research Institute of Mozambique
IPCC	Intergovernmental Panel on Climate Change
MINAG	Ministry of Agriculture
MINED	Ministry of Education
MITADER	Ministry of Land, Environment and Rural Development
RdM	Republic of Mozambique
REDD+	Reducing emissions from deforestation and forest degradation and enhancement of forest carbon stocks

1 Introduction

In Mozambique and other neighbouring countries, there is a strong need to counteract decades of deforestation and forest degradation. New plantations of fast-growing species and maintenance of mature woodlands are activities supported by the REDD+ mechanism (Reducing Emissions from Deforestation, Forest Degradation and Increasing Carbon Stocks) in the United Nations Framework Convention on Climate Change (UNFCCC) (IPCC, 2006) to reduce carbon emissions to the atmosphere, to increase the capacity of forest ecosystems for carbon storage and sequestration and to sustain livelihoods.

Of the natural forest types in central and southern Africa, miombo is the most extensive and also one of the types most subjected to deforestation and degradation (Griscom et al., 2009, Ciais et al., 2011, CEAGRE and Winrock-International, 2016, Jew et al., 2016). Miombo woodland (hereafter referred to as 'miombo forest') is a colloquial term used to describe the most extensive tropical seasonal woodland and dry forest formation in Africa (Campbell et al., 1996, Kutsch et al., 2011, Chidumayo, 2013, Blackie et al., 2014, Jew et al., 2016). About 50% of inland Mozambique forest is miombo forest (Wild and Grandvaux Barbosa, 1967). It provides a wide range of goods and ecosystem services, thus playing an important role for household livelihoods and, moreover, supporting rural communities in climate change mitigation and adaptation.

A number of ways to reduce or reverse deforestation and forest degradation in tropical forests are suggested in the literature (Griscom et al., 2009, MINAG, 2009, FAO, 2010, UNEP, 2014, CEAGRE and Winrock-International, 2016, MITADER, 2016). These include enhancement of carbon stocks and sequestration capacity in biomass and soil through reforestation.

Reforestation can be undertaken using different approaches (Lamb, 2011). Detailed background to the degradation of miombo forest in Mozambique and a description of different reforestation approaches are provided in Section 4.2.1 of this thesis.

2 Research questions

Reforestation using new plantations of fast-growing species and maintenance of mature woodlands in the tropics raise a number of research questions. The focus of this thesis was on how these activities affect carbon stocks and dynamics in soil and vegetation. A large number of studies have demonstrated soil effects of plantations on abandoned farmland (e.g. Li et al., 2012, Cunningham et al., 2015), but there is a lack of knowledge on the effect of plantations compared with degraded or non-degraded miombo forest, including effects on carbon stocks in soil and biomass and on soil fertility. Such knowledge, in particular knowledge of high relevance for specific regions within the country, is required to guide reforestation programmes in Mozambique (Coetzee & Alves, 2005).

In addition to measuring effects on stocks of carbon and nutrients, there is a need to understand the conditions and processes behind such changes. Thus, new studies are required to include measurements of the major components of net primary production, as well as analyses of decomposition of soil organic matter. This is of particular importance when comparing *Pinus* and *Eucalyptus* plantations with miombo forest, since potential effects may derive from different carbon allocation patterns, litter quality and management regimes, or lack of management.

Allometric biomass equations are used to estimate tree biomass from simple non-destructive measurements, *e.g.* stem diameter at breast height, and they are essential tools in any reliable estimation of carbon stocks at ecosystem scale. Such equations have a wide range of applications, for example to support implementation of different reforestation approaches and for monitoring changes in forest biomass at the stand or landscape scale. For example, quantification of the amounts of carbon stored in aboveground biomass is an important component in implementation of the emerging REDD+ mechanisms (Mugasha et al., 2013). The biomass equations should harmonise with the good practice guidance for tree biomass and carbon inventory provided by the International Panel on Climate Change (IPCC, 2006).

In this thesis work, a search was made in the literature to find allometric biomass equations for miombo, *Pinus* and *Eucalyptus* forests of Mozambique. This search identified a need to develop new equations, or select biomass functions from the literature, based on their performance compared with the biomass of trees sampled within the study area of the thesis (the Beira corridor region). The aboveground biomass in this context includes both trees and shrubs, and excludes roots, dead aboveground biomass like litter and fallen branches or stems, and the belowground biomass, which consists of roots (Vashum and Jayakumar, 2012).

3 Aims, objectives and hypotheses

3.1 Aims and objectives

The overall aims of this thesis work were:

- To quantify the impacts of first-rotation, pure plantations of *Pinus and Eucalyptus* compared with mountain miombo forest on carbon stocks and dynamics in soil and biomass within the Beira corridor region, central Mozambique (**Papers I-IV**).
- To develop allometric biomass equations (tools) for estimating total aboveground biomass of trees in lowland miombo forest within the Beira corridor region, central Mozambique (**Paper V**).

The first aim was achieved by studies on first-rotation (ca. 34 years) plantation stands of *Pinus taeda* L (loblolly pine*)*, *Eucalyptus grandis* Hill ex. Maiden (flooded gum), *E. cloeziana* F. Muell. (gympie messmate) and adjacent **mountain** miombo forest (around 1100-1700 m above sea level) located at different sites in the western part of the Beira corridor region of central Mozambique. Specific objectives of these studies were to:

i. Quantify the effects of a first-rotation plantation of *P. taeda* and *E. grandis* plantations on soil organic carbon stocks, nutrient stocks and acidity compared with those of adjacent mountain miombo forest (**Paper I**).

ii. Quantify total ecosystem carbon stocks in soil, litter layer and tree biomass (Table *1*) of first-rotation, mature plantations of *P. taeda* and

E. grandis compared with adjacent mountain miombo, and estimate net ecosystem production of the plantation forests (**Paper II**).

- **iii.** Compare the effects of first-rotation plantations (34-year-old) of *P. taeda* and *E. cloeziana* with those of adjacent mountain miombo with respect to net primary production, and its different components (Table 1) (**Paper III**).
- **iv.** Estimate litterfall and decomposition rates of leaf litter of *P. taeda*, *E. cloeziana* and dominant species in mountain miombo, in order to predict the long-term accumulation of carbon stocks in the soil and litter layer in the different forest types (**Paper IV**).
- **v.** Develop new multi-species allometric models for estimating total aboveground tree biomass (living and dead) in lowland miombo forests within the Beira corridor region in Mozambique (**Paper V**).

Table 1. *Components of total carbon stocks, net ecosystem production and net primary production studied in this thesis.*

Parameter	Carbon components
Total ecosystem carbon stocks	Aboveground live tree biomass (stems, branches and foliage), belowground woody biomass (coarse roots), litter layer and soil organic matter (0-50 cm).
Net ecosystem production	As for total ecosystem carbon stocks
Net primary production	Litterfall, aboveground biomass increment, belowground biomass increment, and fine root production.

3.2 Hypotheses

The hypotheses tested in **Paper I** were that the higher level of production of aboveground biomass (stems, branches and foliage) observed in plantations of *Pinus taeda* and *Eucalyptus grandis* compared with mountain miombo forest leads to: higher soil carbon and nitrogen stocks than in miombo forest (**H1**), with a stronger effect of *E. grandis* than of *P. taeda* (**H2**); decreased stocks of extractable phosphorus as a consequence of increased nutrient demand and uptake in trees (**H3**); and increased soil acidification as a consequence of increased stocks of soil carbon and nutrient accumulation in the biomass (**H4**).

In **Paper II**, the hypotheses tested were that carbon stocks in biomass of mature stands of *P. taeda* and *E. grandis* are greater than those in miombo biomass, but do not differ between the two plantation species (**H5**); and that carbon stocks in plantation biomass comprise a greater proportion of the total carbon stocks than in miombo forest stands (**H6**).

Paper III tested the hypothesis that: net primary production is higher in plantation stands than in miombo (**H7**); net primary production is proportional to basal area across forest types (**H8**); and there is no difference in allocation pattern of carbon to different components of net primary production between forest types (**H9**).

Paper IV tested the hypotheses that: leaf litter in miombo stands decomposes faster than litter in pine or eucalypt plantation stands at the same location (**H10**); substrate quality, not microbial growth rate (as determined by temperature), explains differences in decomposition rate (**H11**); and measured carbon stocks in the litter layer can be explained by observed litterfall and litter decomposition rate over a 34-year stand rotation (**H12**).

4 Background

4.1 Miombo forest - threats and solutions to deforestation and forest degradation

In recent decades, overexploitation of miombo forest in Mozambique and similar Africa countries has caused deforestation and forest degradation and loss of goods and ecosystem services at high rates (Campbell et al., 2007, Ciais et al., 2011, Sitoe et al., 2012a, Jew et al., 2016). According to CEAGRE and Winrock-International (2016), between 2000 and 2012 about 138,000 hectares of forest were lost annually in Mozambique. According to that study, deforestation and forest degradation was responsible for approximately 4.4 million tons of carbon being released per year to the atmosphere (assuming that 1 ton of carbon represents 3.67 ton of CO_2), of which nearly 80% came from miombo forest, regardless of type (CEAGRE and Winrock-International, 2016). A large proportion (>75%) of the deforestation and forest degradation in Mozambique in general is directly caused by agriculture practices and expansion (mainly shifting cultivation), wood fuel production (charcoal) and logging (especially illegal activities), often acting in combination (CEAGRE and Winrock-International, 2016).

The central part of Mozambique, where the Beira corridor is located, is the region where miombo forest is most threatened by deforestation and forest degradation, compared with other development corridors. As defined by the Mozambique Development Strategy (RdM, 2014), development corridors are regions where integrated activities are carried out to promote local development. Four development corridors (Beira, Nacala, Limpopo and Maputo) have been defined at the national level. The integrated activities include forestry, agriculture, tourism, fisheries and mining, among others, to achieve social, economic and environmental goals.

The rate of deforestation and forest degradation in the Beira corridor region (0.36% per year) is 57% higher than the mean rate for the whole country (0.23% per year) and is 112% higher than the average rate estimated for the four development corridors in Mozambique (0.17% per year) (CEAGRE and Winrock-International, 2016). Some degraded miombo sites, including other wooded areas, will need active intervention to recover the production capacity of goods (*e.g.* timber and fuel) and ecological functions (*e.g.* carbon storage, nutrient cycling and maintenance of wildlife habitats).

Incentives to counteract deforestation and forest degradation have been promoted in Mozambique, particularly under the national reforestation strategy (MINAG, 2009) and the national strategy for reducing emissions from deforestation and forest degradation (REDD+) (MITADER, 2016). These interventions are in line with *e.g.* the UN convention on climate change (UN, 1992b) and the UN convention on biodiversity (UN, 1992a).

Several ways to reduce or reverse deforestation and forest degradation in tropical forests are suggested in the literature (Griscom et al., 2009, MINAG, 2009, FAO, 2010, UNEP, 2014, Sitoe and Guedes, 2015, CEAGRE and Winrock-International, 2016, MITADER, 2016). Within the forestry sector, the interventions can be of two kinds (FAO, 2010): i) interventions aiming to conserve forest carbon stocks through reduction of deforestation and forest degradation, for example by reinforcement of sustainable practices of forest management and use and integrated fire management and ii) interventions aiming to enhance carbon stocks and sequestration capacity of degraded or deforested area (biomass and soil) through reforestation or afforestation.

Reforestation was the focus of the work described in this thesis. According to the Ministry of Agriculture in Mozambique, there are about 7 million ha of land suitable for reforestation in the country (MINAG, 2009). Based on available data, the current area of forest plantations may be less than 100,000 ha (Coetzee and Alves, 2005, MINAG, 2009, DNTF, 2014, 2015), but it is increasing to some extent. By 2030, the country's aim is to establish 1.3 million hectares of new forest plantations (MINAG, 2009), which is more than a 10-fold increase compared with the current situation.

Pinus and *Eucalyptus* are the genera most frequently planted in Mozambique and in Africa in general (FAO, 2001, Chamshama et al., 2009, MINAG, 2009). They are attractive for use in forest plantations for a number of reasons (Lugo and Brown, 1993, FAO, 2001, Dohrenbusch, 2011). For example, they are easy to manage and have rapid adaptability, rapid growth and high productivity of wood, and consequently high carbon sequestration rate. Reforestation in Mozambique generally takes place on deforested or degraded miombo forest sites, including degraded agricultural land, thickets and marginal land (less fertile soils for growing food or land located on steep slopes) (MINAG, 2009, Maússe-Sitoe et al., 2016, MITADER, 2016).

In the following, degraded forest, or "high-utilisation sites" according to terminology adopted by Jew et al. (2016), is defined as a forest which has lost much of its original biomass or carbon stocks and net primary production (adapted from Lamb and Gilmour, 2003, IPCC, 2006, Thompson et al., 2013, Scott et al., 2015, Jew et al., 2016). This definition also denotes reduced forest cover, as long as the site can be considered a 'forest' (Tavani et al., 2009, Sitoe et al., 2012b). Degraded forests can differ in many regards, including: i) causes or intensity of the causes that left a particular site in a degraded state; ii) ecological attributes of a particular forest (*e.g.* structure and species composition remaining, seedlings and seed dispersal, soil conditions) (Lamb and Gilmour, 2003, Lamb, 2011); iii) carbon storage capacity in aboveground tree biomass (Jew et al., 2016); and iv) capacity to recover unaided if further disturbance can be prevented (Lamb et al., 2005).

4.2 Reforestation

4.2.1 Approaches

Reforestation is one of the ways to counteract deforestation and forest degradation in tropical zones, and hence to tackle climate change. Reforestation can be undertaken using three main approaches (Lamb, 2011): i) restoration, ii) rehabilitation and iii) monoculture plantation. Figure 1 shows a conceptual diagram of these three reforestation approaches. Point A in Figure 1 represents an undisturbed forest ecosystem, *i.e.* an original native forest, which has a certain level of biomass, structure, productivity and biological diversity. Forest degradation can lead state A to change to states B, C, D or E, which represent different levels of forest degradation (Lamb and Gilmour, 2003, Lamb, 2011).

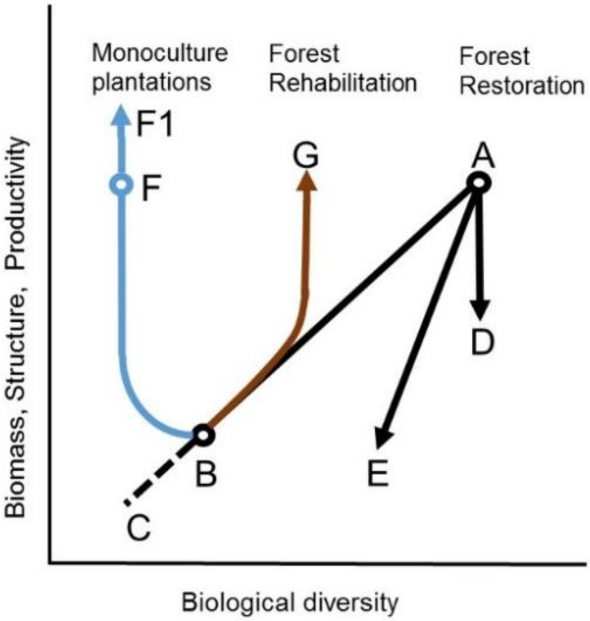

Figure 1. Conceptual diagram of reforestation, showing different levels of loss of biomass, structure and productivity and of biological diversity (from pristine state A to B, C, D and E), and the relationship between forest restoration, rehabilitation and monoculture plantations (adapted from Lamb and Gilmour, 2003, Lamb, 2011).

The aim of forest restoration is to assist the recovery of a degraded forest ecosystem in order to re-establish the biomass, structure, productivity and biological diversity of its native condition (Lamb and Gilmour, 2003, Lamb, 2011). Forest restoration in practice aims to bring back the original forest cover by promoting a transition from states B, C, D or E to state A (Figure 1). Natural recovery to state A can occur from states D and E, but the recovery from the conditions at states B or C can be more difficult or, at best, very slow, even if further disturbance can be prevented (Lamb and Gilmour, 2003, Lamb, 2011). In states B or C, monoculture plantations or forest rehabilitation with fast-growing non-native (exotic) species might be the most efficient way to reverse forest degradation (Lamb, 2011).

In contrast, monoculture plantation aims primarily to re-establish the biomass and productivity of former degraded forest (states B or C) (Lamb and Gilmour, 2003). Forest rehabilitation, on the other hand, lies between forest restoration and monoculture plantation, and aims to re-establish biomass and productivity of the former degraded forest and some, but not necessarily all, of the biological diversity that originally existed at the site (state A) (Lamb and Gilmour, 2003, Lamb, 2011).

In theory, these three approaches to reforestation can be applied to any form of degraded forest (Lamb and Gilmour, 2003). All three attempt to develop productive forests (biomass), but they differ in the extent to which the biological diversity or structural complexity of former forest is regained, and in their capacity to restore supply of both goods and ecosystem services (Lamb, 2011). In practice, the choice of approach is influenced by a number of factors, including ecological, financial, social and cultural aspects, and forest governance aspects (Le Houerou, 2000, Lamb and Gilmour, 2003, Chamshama et al., 2009, Bauhus et al., 2010, Pokorny et al., 2010, Lamb, 2011, Landry and Chirwa, 2011, Wortley et al., 2013, Cunningham et al., 2015, Maússe-Sitoe et al., 2016).

4.2.2 Sustainable biomass production

Monoculture plantations with fast-growing tree species are prone to rapid productivity decline, due to their high nutrient demand, unless soil fertility level is restored (Lamb, 2011). Several factors affect the sustainability of monoculture plantations of fast-growing tree species during the second or subsequent rotations (Heilman and Norby, 1998, Brandtberg, 2001, Zewdie, 2008, Lamb, 2011, Onyekwelu, 2011, Pellegrini, 2016). Nutrient depletion in the soil is due to uptake by trees, and the nutrient removal with harvested biomass, which can be particularly high in short-rotation plantations (*e.g.* less than 10 years, which is commonly the case for pulpwood plantations). Additional nutrient losses can occur due to other management practices, *e.g.* repeated or intense use of fires.

Besides nutrient addition by fertilisation, there are other management practices that aim at maintaining the long-term site productivity of forest plantations. One example of a good practice mentioned by Chamshama et al. (2009) is to confine harvesting of forest products to stem wood and avoid burning or raking the nutrient-rich slash after harvesting. Another good practice is to minimise physical soil damage such as soil compaction and erosion by careful planning of logging and forwarding tracks (tramlines) at the site.

4.2.3 Climate change mitigation, and enhancement of biological diversity

In most cases, the aim of monoculture plantations of non-native species is to supply economically profitable wood products for the market (*e.g.* sawn wood, pulpwood) (FAO, 2001, Chamshama et al., 2009, MINAG, 2009). However, monoculture plantations can also contribute substantially to mitigating climate change and can serve as a means for rehabilitation of degraded forests.

Monoculture plantations can support conservation of biological diversity, through *e.g.* supplying habitats for wildlife and providing the conditions for native species recolonisation (Geldenhuys, 1997, Chazdon, 2003, Lamb and Gilmour, 2003, Chamshama et al., 2009, Bauhus and Schmerbeck, 2010, Lamb, 2011).

From a climate perspective, the role of monoculture plantations of non-native species can be increased by promoting attractive or efficient ways to use the biomass harvested, which includes the use of residues in the plantations in order to reduce the pressure on miombo forest and to minimise the carbon release into the atmosphere. Thus, the role of monoculture plantations can be increased through, for instance, the use of structural timber in local construction work and in furniture making; generation of firewood and charcoal; use of surplus forest plantation materials to produce wood pellets for domestic use or export; and use of biochar (Lamb, 1998, Canadell and Raupach, 2008, Sitoe, 2009, Porsö et al., 2016, Gustavsson et al., 2017, Xu et al., 2017).

From a biological diversity perspective, monoculture plantations of non-native species can play a role by promoting transition of the degraded forest ecosystem from state F to state G (Figure 1). For example, increased spacing of tree plantings, increased rotation length and direct protection of understorey vegetation are possible means to promote the diversity of understorey plants in plantations.

5 Material and methods

5.1 Study area

The study area lies within the Beira development corridor region (latitude 18°S - 20°S), comprising approximately 29,000 km^2, located within the provinces of Manica and Sofala in central Mozambique (Figure 2). Two sub-regions of the Beira development corridor were defined for the studies.

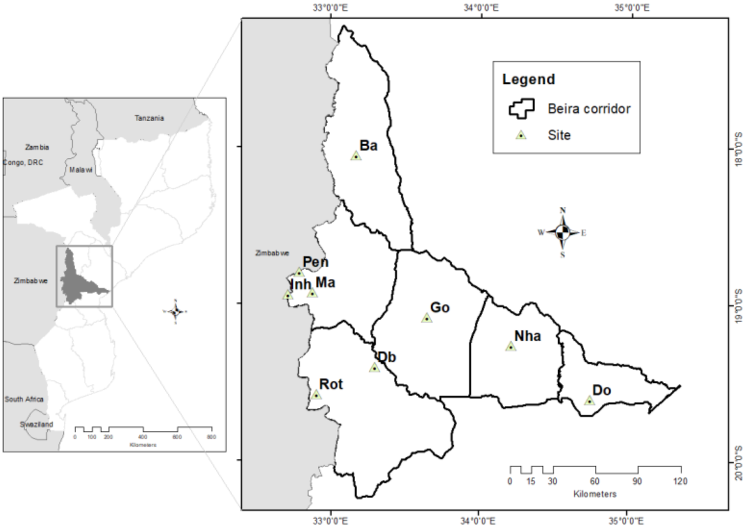

Figure 2. Location of the Beira corridor study area in central Mozambique. Do is Dondo district, Nha is Nhamatanda district (both in Sofala province in the east). Go is Gondola district, Db is Dombe village in Sussundenga district, Ma is Manica district and Ba is Báruè district (all in Manica province to the west). Inh is the Inhamacari Forest Unit (managed by Machipanda Research Centre of Eduardo Mondlane University), and Pen and Rot are the Penhalonga and Rotanda Forest Units, respectively (both managed by the IFLOMA Company). All three forest units lie within the Western highlands of Manica province (Map: Lisboa Sa Nogueira).

Sub-region 1 was represented by three sites, the Inhamacari (Inh), Rotanda (Rot) and Penhalonga (Penh) forest units (Figure 2), all of which are located within the Western highlands of Manica province, which is part of the Cordillera of Chimanimani (African mountainous element), one of most important centres of mega-biodiversity in Mozambique. The terrain at the sites is mostly steeply sloping, with elevation ranging from 1100 to 1700 m above sea level (a.s.l.). The vegetation can be characterised as a mosaic dominated by mountain miombo (native forest) and monoculture plantations, mostly with *Pinus* and *Eucalyptus* species. The Inhamacari, Rotanda and Penhalonga sites were used for the studies in **Papers I** and **II**, while only the Inhamacari site was used for the studies in **Papers III** and **IV**.

Sub-region 2 was represented by six other sites, *i.e.* Dondo district (Do), Nhamatanda district (Nha), Gondola district (Go), Dombe village (Db) and Manica district (Ma) (Figure 2). These sites belong to a region of low altitude in the Beira corridor study area, below 1100 m a.s.l. and mostly between ~50 and 720 m a.s.l. All six sites were used for the study in **Paper V**. The dominant vegetation type at all sites is lowland miombo.

The area covered by each miombo type studied was not determined but, based on a map produced as part of **Paper V,** around three-quarters of the Beira corridor study area is lowland miombo forest. *Brachystegia spiciformis* Benth. (Leguminosae), *Julbernardia globiflora* (Benth.) Troupin (Leguminosae), *Uapaca kirkiana* Müll. Arg. (Phyllanthaceae), *Pericopsis angolensis* [Baker] Meeuwen (Leguminosae), and *Parinari curatellifolia* Planch. Ex. Benth (Chrysobalanaceae) are some of the dominant tree species in both lowland miombo and mountain miombo forests.

Although similar with respect to dominant trees species, mountain miombo and lowland miombo forests are structurally different forest types, at least in the Beira corridor study area (Figure 3). Actually, seven different types of miombo forests have been distinguished in Mozambique, based on physiognomy and structure (MINED, 1986). The total height of the dominant tree species in the lowland miombo forest generally falls within the range 10-15 m (Sitoe, 2005, Sitoe, 2009), with large trees reaching 25 m height (Mate et al., 2014). In contrast, mountain miombo forest is characterised by short trees, with dominant height around 7 m (Pereira et al., 1999) and with few trees reaching 12 m.

Forest plantations in the study area consist mostly of monoculture plantations of *Pinus taeda*, *P. patula***,** *P. elliottii*, *Eucalyptus grandis*, *E. cloeziana* and *E. camaldulensis*. All these species except *E. cloeziana* are also widely planted in neighbouring countries, *e.g.* Zimbabwe and South Africa (FAO, 2001, Mujuru et al., 2014, Dube and Mutanga, 2015).

Figure 3. Inside a) mountain miombo forest and b) lowland miombo forest, within the Beira corridor region, central Mozambique (Photo (b) taken by A. Sitoe).

The plantation forests examined in this study were pure *P. taeda*, *E. grandis* and *E. cloeziana* stands located in sub-region 1 and established between 1977-1980 (Adam et al., 1991). These stands represent the first generation of large-scale industrial forest plantations established in the study area, and in Mozambique in general. The mean age of the plantations studied was 34 years during the assessment year 2012 (± 2 years uncertainty), which is a calculation based on oral sources (senior staff at Machipanda Research Centre and IFLOMA) and subsequently confirmed through a Sida (Swedish International Development Cooperation Agency) evaluation report of the Mozambique-Nordic Agricultural Programme (MONAP) (Adam et al., 1991).

The plantations have not received fertiliser over the years. Moreover, they are better protected against cutting, pruning and fires compared with the adjacent mountain miombo forest. However, the mountain miombo forest surrounding the three forest units (Penhalonga, Rotanda and Inhamacari) is relatively better protected and is less degraded than most other miombo forest in the region.

According to the Köppen-Geiger classification, the climate in the Beira corridor study area ranges from tropical savannah (Aw) in the eastern part (sites Do, Nha and Db; Figure 2) to humid subtropical (Cwa) with dry winter and warm summers in the central part (sites Ma, Go and Ba) and temperate with dry winters and warm summers (Cwb) in the western part (sites Inh, Pen and Rot) (Peel et al., 2007, Climate-Data.org, 2016). Detailed descriptions of the climate at the study sites can be found in **Paper I** (sub-region 1) and **Paper V (**sub-region 2).

5.2 Study design

Forest stands that met the following criteria were selected as the research objects in **Papers I-IV**: (i) forest stands of first-rotation *Pinus taeda, E. cloeziana* and *E. grandis* plantations and miombo stands in close proximity to one another (Figure 4), (ii) similar soil type and (iii) former land use similar to that in adjacent miombo forest stands. In the field, these criteria were implemented with the help of senior staff from the IFLOMA Company (M. Mariano, personal communication, Oct. 2012) and the Machipanda Forest Centre of Eduardo Mondlane University (A. Esequias, personal communication, Sept. 2012).

For Papers I-II, three sites in the Western highlands in Manica province were used, *i.e.* the Inhamacari (Inh), Penhalonga (Pen) and Rotanda (Rot) forest units (Figure 2). At this regional scale, forest stands of P. *taeda* and *E. grandis* plantations were selected for study, since mature *E. cloeziana* was found only at one site (Inh). The three sites were considered as blocks in a randomised block design (n=3) and, at each site, a single study plot (30 m x 30 m) was established in each of the three forest types, *i.e.* mountain miombo, P. *taeda* plantation and E. *grandis* plantation.

For **Papers III** and **IV,** which involved studies on forest type differences in biomass, growth, litter production and rate of decomposition of leaf litter, the research was confined to the Inhamacari site, where Machipanda Research Centre provided logistics support to ensure monitoring of litterfall and other repeated measurements. Three plots (30 m x 30 m) of each forest type (mountain miombo, *Pinus taeda* and *Eucalyptus cloeziana*) were selected for these two studies, following the same criteria (i)-(iii) as described above. Thus, the studies in **Papers I-II** and **Papers III-IV** shared one plot of mountain miombo forest and one plot of *Pinus taeda* at Inhamacari Forest Unit.

Figure 4. Illustration of (left foreground) a mountain miombo in the Western highlands of Manica province, within the Beira corridor study area, central Mozambique (left), located adjacent to (right) an approximately 34-year-old pure plantation of *Pinus taeda* (Photo: Bengt Olsson).

5.3 Field and laboratory work

5.3.1 Study of soils (**Papers I** and **II**)

In each of the three plots at Inhamacari, Rotanda and Penhalonga, stem diameter at breast height (DBH) was measured on all trees and shrubs with DBH >5 cm and each individual was identified at species level in the field with the help of a botanically skilled technician. Soil and litter layer were sampled at 10 spots in each plot. The sampling spots were distributed in a systematic way to estimate the mean of the plot. A 15 cm x 15 cm frame was used for the litter layer sampling. Soil cores were collected using an auger (28 mm diameter) from two depths (0-10 and 10-30 cm), and samples were extracted after pooling together the cores in each layer. For the deeper layers (30-50 cm), soil samples were collected from a single soil profile pit excavated in each plot. In total, nine soil samples (three sites x three soil layers) were collected from each forest type (mountain miombo, *P. taeda* and *E. grandis*) for chemical analyses. A soil inventory (**Paper I**) and forest inventory (**Paper II**) were carried out. Laboratory analyses of soils were performed according to a protocol by Westerhout and Bovee (1985). The main focus of the analyses was determination of soil organic carbon stocks, but soil pH (H_20), exchangeable base cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+), exchangeable acidity ($Al3^{+}$ $^{+}$ H^+) and soil texture were also determined (**Paper I**). Soil analyses were performed at the Faculty of Agronomy and Forest Engineering, University Eduardo Mondlane (UEM) in Mozambique.

5.3.2 Study of forest stands (**Papers III-V**)

The studies reported in **Papers III** and **IV** were performed at the Inhamacari site. Three permanent inventory plots of 30 m x 30 m (0.09 ha) were established for each forest type studied (mountain miombo forest, and *Pinus taeda* and *E. cloeziana* plantations), giving a total of nine plots in the study.

*Changes in stem diameter (DBH) growth (**Paper III**)*

In each of the nine study plots at Inhamacari, mean annual diameter at breast height (DBH) increment was estimated based on repeated measurements, in March 2013 and July 2014, in each of the sampling plots using existing methods (Sitoe, 1999, Bowman et al., 2013). All trees (DBH ≥5 cm) were identified to species level in the field with the help of a botanically skilled technician and were given a unique code using paint. Diameter at breast height was measured using a diameter tape. No mortality was observed during the 16 months of forest monitoring.

The monitoring period exceeded one year (16 months) due to logistical constraints. However, the period April-July 2014 was the beginning of the dry season, and tree growth can therefore be expected to have been lower than the annual average. Using the time interval of 16 months may thus have led to underestimated tree growth. The data collected were also used *e.g.* to estimate basal area of each forest type and tree density (stems per hectare), where trees were defined as all woody plants taller than 2 m (Frost, 1996).

*Aboveground fine litterfall (**Paper III**)*

Aboveground fine litter was collected continuously over a year using square litter traps (50 cm x 50 cm, approx. 20 cm deep), constructed from window screen (with a mesh size of 1.2 mm) (Muller-Landau and Wright, 2010). In each study plot, 15 litter traps were installed suspended at 25 cm above the ground, giving a total of 45 traps per forest type. The collected litter included tree foliage, reproductive parts (flowers, fruits, seeds and supporting structures/pedicels) and twigs (≤5 mm diameter), but excluded herbaceous material and branches >5 mm (Clark et al., 2001a). Aboveground fine litter was collected monthly, pooled per sampling plot, labelled and stored at -18 °C. Prior to determination of mass, the samples were dried in the laboratory at 65 °C to constant weight.

*Fine root production and turnover rate (**Paper III**)*

Fine root (≤2 mm diameter) production was monitored in the 0-15 cm soil layer, based on sampling using the in-growth core method (Majdi et al., 2005, Finér et al., 2011, Gwenzi et al., 2011, Addo−Danso et al., 2016), over the period October 2012 to January 2013. The root inclusion net method was tested but was inapplicable due to the physically hard soils at our study site. In each sampling plot, five sampling points were randomly located, totalling 15 per forest type. At each sampling point, a soil core was collected with a 55 mm diameter steel corer. All roots were removed by hand in the field, and the root-free soil was then replaced in the in-growth mesh bag (1 mm mesh size, 150 mm length and 50 mm diameter).

The mesh bags were name-tagged, sealed and buried in the soil, and a litter layer was placed on top to hide the cores. The measurements included two sampling series at approximately seven-month intervals over the 15-month period. In the laboratory, the fine roots were separated manually from the soil and washed in a 0.25 mm mesh sieve, to remove soil and other impurities. Live and dead roots were not distinguished in this study. Samples were oven-dried at 65 °C to constant weight and weighed in an analytical precision scale (Mettler digital laboratory scale model PE160, precision 0.001 g). In this thesis work, the fine roots production was probably underestimated because of two factors. First, the ingrowth core method used, generally underestimates fine root production (Lukac and Godbold, 2010, Finér et al., 2011, Osawa and Aizawa, 2012, Addo−Danso et al., 2016), compared to the root inclusion net method (Lukac and Godbold, 2010). Second, because root production below 15 cm in the soil was neglected.

*Leaf litter decomposition study (**Paper IV**)*

Leaf mass loss was estimated by litter bag technique (Bärlocher, 2007, Karberg et al., 2008). The leaf litter material used for analysis was collected fresh on the forest floor at the time when the litterfall of all tree species in the study area is normally at its peak (May-June). The material was air-dried before incubation. Litter bags for incubation in the field were made by placing fixed amounts (1.8 g per bag) of dry litter in nylon mesh (1.0 mm) bags fitted with plastic identity tags. The litter bags contained five different leaf substrates, *i.e*. litter of *Pinus taeda, Eucalyptus cloeziana, Brachystegia spiciformis* and *Uapaca kirkiana,* and a mixture of litter from the six dominant miombo species (*B. spiciformis, Julbernardia globiflora, Pericopsis angolensis, U. kirkiana, Parinari curatellifolia* and *Bridelia micrantha*). The bags were placed in field plots within stands of their respective tree species in October 2012, in the same plots as used for litterfall studies.

For each litter type, 25 bags were placed in each of the three sampling plots, distributed equally between five stations, and covered with a thin layer of fresh litter to make them less visible. On five occasions distributed over 13 months, one bag per station was collected and stored at -18 °C until preparation of all samples took place. In the laboratory, the leaf litter was carefully separated from the mesh bags and was manually cleansed from roots and mineral soil particles that had entered the bags. The cleansed litter samples were dried at 60 °C for around 24 hours to constant weight. All mass determinations were made using the same precision balance (Adam Lab Analytical Balance PW254, precision 0.0001 g). Carbon content in litter was assumed to be 50% of dry mass.

The assessment of leaf litter decomposition rate also included soil temperature measurements, to estimate the occurrence and magnitude of systematic differences in soil temperature between stand types. Soil temperature was measured using small button-shaped temperature loggers of type Thermotrack PC Cinco v7 (21G; serial number 2100-0000-315A-5D81), with resolution 0.5 °C and precision ± 1 °C according to the manufacturer. The loggers were buried in the O-horizon underneath a layer of fresh litter, similarly to the litter bags. Temperature data were recorded every 4 hours, over 217 days, from June 2014 to January 2015.

5.3.3 Destructive sampling of biomass for selecting allometric equations for mountain miombo, *Pinus* and *Eucalyptus* forest (**Paper II**)

Since allometric biomass equations are essential tools for estimating carbon stocks in tree biomass, identifying and applying the most accurate biomass equations was an essential step to achieve the objectives referred to in **Papers I, II** and **III.** To select the most accurate biomass equations from the literature, destructive sampling for biomass determination was carried out (**Paper II**). The sampling followed standard field sampling procedures and laboratory work recommended for the construction of allometric equations of biomass (Picard et al., 2012, Smith et al., 2014). Destructive sampling was carried out in a period of peak foliage (January-June). Due to legal constraints, it was only possible to select trees for destructive sampling at the Inhamacari site. In total, 29 trees were sampled in *P. taeda* plantation, 29 trees in *Eucalyptus spp.* plantation (*E. grandis* and *E. cloeziana*) and 33 trees in mountain miombo forest (Table 2). The range of diameter at breast height and the variation in total height of the sampled trees were considered to be representative of each forest type sampled.

Table 2. *Attributes of the trees sampled and used to test and select the most adequate biomass equation for estimating aboveground carbon stocks in mountain miombo,* Pinus taeda *and* Eucalyptus grandis *or* Eucalyptus cloeziana *in the Western highlands of Manica province, Mozambique. DBH is stem diameter measured at 1.30 m height above ground level.*

Parameter	Forest type		
	Mountain miombo	*Pinus taeda*	*Eucalyptus* spp.¥
DBH range (cm)	5-36	5-39	5-74
Total height (m)	4-12	6-27	8-39
Number of trees sampled	33	29	29

¥ Individuals of *E. cloeziana* were included in the sampled tree in similar proportions to individuals of *E. grandis*, which were the *Eucalyptus* species studied here.

Tree species selection/prioritisation for destructive sampling for biomass determination in miombo stands was carried out based on importance value index, which is a measure of dominance of species in a particular area (Dash, 2001, Agarwal, 2008, Ribeiro et al., 2013, Kacholi, 2014). Importance value index was calculated by adding together the relative frequency, relative abundance (N ha^{-1}) and relative basal area (m^2 ha^{-1}) for each tree species. The six tree species determined as being the most dominant in mountain miombo forest (>85%) were then included in the destructive sampling. These dominant tree species were the same as those included in the decomposition study described in the previous section.

The biomass of the sampled trees was used to select one candidate biomass equation that matched the trees at the actual site as closely as possible (Figure 5). For mountain miombo, there were five candidate equations (Chamshama et al., 2004, Ryan et al., 2011, Chidumayo, 2013, Mugasha et al., 2013, Kuyah et al., 2014); for *P. taeda* there were four candidate equations (Brown, 1997, Brown and Schroeder, 1999, Jenkins et al., 2003, Gonzalez-Benecke et al., 2014); and for both *Eucalyptus* spp. three candidate equations were tested, one by Zunguze (2012), one by Eamus et al. (2000) and one by O´Brien (1998; *cit*. Zianis and Mencuccini (2004). All equations tested use tree diameter at breast height in predicting variable dry weight.

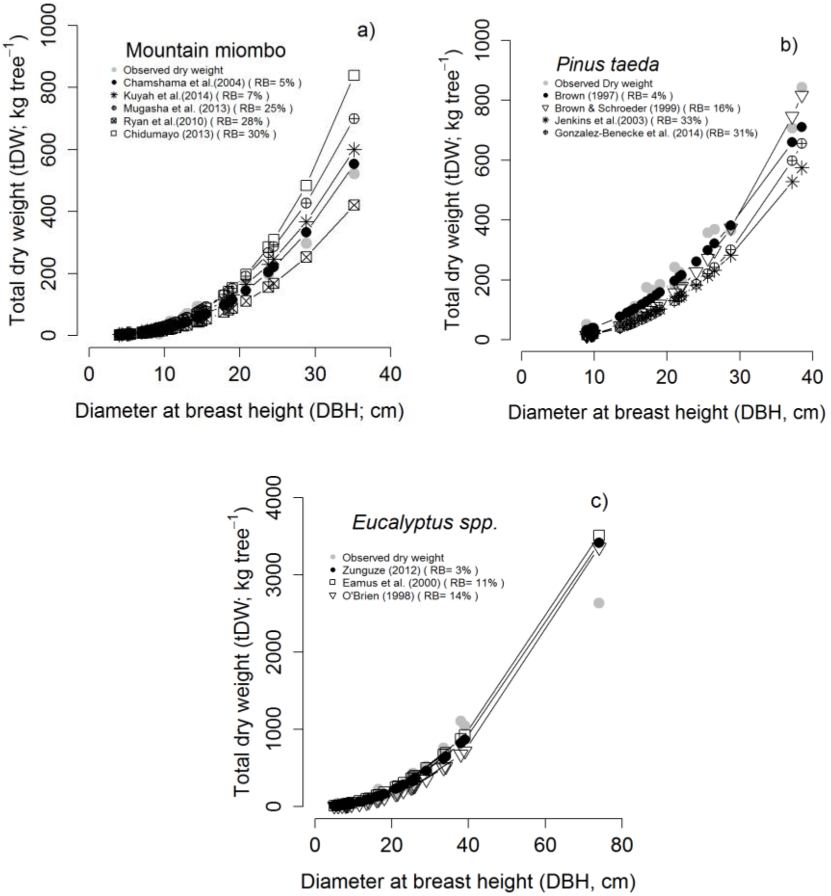

Figure 5. Fitted line plot of the relationship between total dry weight (stems, branches, and foliage) and stem diameter at breast height (DBH, at 1.3 m above ground level) of each candidate biomass equation tested for: a) mountain miombo forest, b) plantations of *Pinus taeda* and c) plantations of *Eucalyptus* spp. (*E. grandis* and *E. cloeziana*). RB is relative bias, which indicates the magnitude of deviation of total dry weight (tDW) predicted in relation to total tDW measured for each individually weighed tree (●).

Generalised allometric models that had the best fit to directly measured dry weight data were selected (Table 3) based on lowest mean absolute percentage error (MAPE; Tofallis, 2014, de Myttenaere et al., 2016), average bias (AB), an otherwise goodness-of-fit index (Maydeu-Olivares and García-Forero, 2010, Sitoe et al., 2014), root mean square error (RMSE; Fayolle et al., 2013, Ngomanda et al., 2014) and relative bias (RB; Chidumayo, 2013, Chave et al., 2014). Figure 5 shows the fitted line plot of the relationship between dry weight and DBH for each biomass equation and forest type tested. Only RB results are given here; the performance of the remaining parameters is given in **Paper II.**

Table 3. *Allometric biomass equation selected to predict total aboveground carbon stocks for mountain miombo forest, plantations of* Pinus taeda *and plantations of* Eucalyptus spp. *(*E. grandis *or* E. cloeziana*) in the Western highlands of Manica province, Mozambique. The value of adjusted R-squared denotes the degree of precision of each selected biomass equation.*

Forest type	Equation	Source	Diameter range (cm)	Adj. R^2 (%)	p-value
Mountain miombo	$tDW^{\dagger} = 0.063*(DBH^{\S})^{2.553}$	Chamshama et al. (2004)	1-50	99	<0.0001
P. taeda	$tDW = Exp(-1.170 + 2.119*Ln(DBH))$	Brown (1997)	2-52	98	<0.0001
Eucalyptus spp.	$tDW = 0.339*(DBH)^{2.142}$	Zunguze (2012)	5-74	95	<0.0001

†Total dry weight of individually weighed tree (kg). §Diameter measured at 1.30 m height above the ground surface.

The allometric equations listed in Table 3 were selected to determine the total (stem, branches and foliage) dry weight per tree (tDW, kg) from the stem diameter at breast height data (DBH, cm at height 1.3 m).The performance evaluation of the candidate biomass equations found in the literature (**Paper II**) relating total dry weight per tree to diameter (DBH) resulted in the selection of best fit (Table 3): For mountain miombo, the equation developed by Chamshama et al. (2004) in Tanzania was selected, for *P. taeda* the equation proposed for conifer forests growing in tropical zones by Brown (1997) was used, while for *E. grandis* we selected the equation by Zunguze (2012), suggested for *Eucalyptus* spp. (*E. grandis* or *E. cloeziana*) in Manica province (Mozambique) was selected. The number of trees used to fit each of these selected models is given in Table 2. The selected equations (Table 2) are able to predict aboveground biomass, and hence aboveground carbon stocks, with a high degree of precision at sub region 1, *i.e.* high adjusted R-squared (Table 3), within limits of the Beira corridor study area.

5.3.4 Destructive sampling of biomass for developing biomass equations for lowland miombo forest (**Paper V**)

New equations were constructed, one that uses stem diameter at breast height (DBH) as the predicting variable and another that uses stump diameter (SDI). The DBH equation is intended to estimate total aboveground live biomass (*i.e.* in wood in stems and branches, and in foliage) for a mixture of lowland miombo tree species, based on measurements of stem diameter at breast height. The SDI equation is intended to estimate biomass of harvested trees, from measurements of stump diameter, and thus reconstruct the former biomass/carbon stocks of lowland miombo forest subjected to logging or harvesting.

Table 4. *Main characteristics of the trees sampled in the Beira Corridor study area in Mozambique. DBH is stem diameter at breast height measured at 1.3 m, and SDI is stump diameter measured at 0.1-0.3 m above the soil surface.*

Parameter	Description
DBH range (cm)	5-53
SDI range (cm)	6-58
Total height range (m)	3-26
Construction dataset	155
Validation dataset	32
Total sampled trees	187

Destructive sampling was carried out prior to the start of this thesis work (2009-2012), in sub-region 2, *i.e.* at sites Do, Nha, Go, Db, Ma and Ba (Figure 2). The destructive sampling followed standard field sampling procedures and laboratory work recommended for the construction of allometric equations of biomass (Picard et al., 2012, Smith et al., 2014) (**Paper V**). Field sampling resulted in a total of 187 trees (Table 4), excluding biased trees, of which 155 were used as the construction dataset and the remaining 32 as the validation dataset, *i.e*. an external dataset to measure the fit between predicted and observed dry weight. The sampled trees were considered to be representative of the tree size (diameter and total height) and species composition of lowland miombo forest in the Beira corridor study area. The prediction performance of the two new was evaluated using the construction dataset and the validation dataset. The process included assessment of the linear regression assumptions (linearity, homoscedasticity and normality), average bias (goodness-of-fit index) (Maydeu-Olivares and García-Forero, 2010, Sitoe et al., 2014) and root mean square error (Fayolle et al., 2013, Ngomanda et al., 2014).

As part of evaluating the adequacy of the DBH- and SDI-based equations developed in **Paper V**, their predictive accuracy was compared with that of allometric models, mainly allometric equations developed for other miombo forests, which were taken from the literature. Eight relevant DBH-based models developed for other areas were tested (Brown, 1997, Chamshama et al., 2004, Pearson et al., 2005, Ryan et al., 2011, Chidumayo, 2013, Mugasha et al., 2013, Kuyah et al., 2014, Kachamba et al., 2016, Mugasha et al., 2016), but only one SDI-based model found in the miombo literature (Chamshama et al., 2004). The predictive accuracy of these candidate biomass equations found in the literature was compared with that of the DBH- and SDI-based models developed here using relative bias (RB; Chidumayo, 2013, Chave et al., 2014).

5.4 Calculations of carbon stocks, net ecosystem production, net primary production and litter decomposition rate

5.4.1 Soil carbon stocks (**Paper I**)

Soil carbon stocks, including nutrient stocks (soil organic carbon, total nitrogen and extractable soil phosphorus) per unit area and soil layer (Mg ha^{-1}) were calculated as the product of bulk density, soil layer thickness (0-10 cm, 10-30 cm and 30-50 cm) and the concentration of each element per unit dry mass. Total element stocks at plot level were calculated as the sum of stocks in all layers assessed. Soil bulk density (g cm^{-3}) was estimated per soil layer using a general pedotransfer function (Post and Kwon, 2000, Guo and Gifford, 2002, Paul et al., 2002). Reference values available for comparable sites in the miombo region (King and Campbell, 1994, Mujuru et al., 2014) were used to confirm the estimated bulk density. Further assumptions made for the estimation of bulk density are described in detail in **Paper I**.

The litter layer carbon stock (Mg ha^{-1}) was estimated by assuming that carbon represented 37% of the dry mass, according to the protocol of the Intergovernmental Panel on Climate Change (IPCC, 2006). With exclusion of the litter layer, the estimation of the carbon stocks for the remaining parameters (*i.e*. stems, branches, fine roots, coarse roots and foliage), assumed that carbon comprises 50% of biomass (Brown, 2002, Grace et al., 2006, Mujuru et al., 2014).

5.4.2 Total ecosystem carbon stocks (**Paper II**)

Total ecosystem carbon stocks were calculated for each forest type (mountain miombo, P. *taeda* and E. *grandis*) by summing the carbon stocks in the four carbon pools (Mg ha^{-1}) under study using the equation:

$$TECS = CS_{AGB} + CS_{BGB} + CS_{LM} + SOC \quad \text{(Eq. 1.)}$$

where TECS (Mg ha^{-1}) is total ecosystem carbon stocks, C_{AGB} (Mg ha^{-1}) is carbon stocks within aboveground tree biomass, C_{LM} (Mg ha^{-1}) is carbon stocks in the litter layer, SOC (Mg ha^{-1}) is soil organic carbon and C_{BGB} (Mg ha^{-1}) is carbon stocks within belowground woody biomass. Belowground woody biomass consisted of coarse roots, *i.e*. roots with diameter >2 mm, as suggested by Brunner et al. (2015).

The amount of carbon in the understorey vegetation (grasses and herbaceous plants) and in dead trees was not assessed in this thesis work, and was therefore not included in the calculations of total ecosystem carbon stocks and net ecosystem production. In previous studies (Sitoe, 2009, Ribeiro et al., 2013) in lowland miombo forests in Mozambique, these carbon pools explained 3% and 9% of total carbon stocks, respectively. These observations suggest that total ecosystem carbon stocks in mountain miombo studied here can probably be underestimated by the same order of magnitude.

The stock of carbon of each component in Equation 1 was estimated as the average of the three sampled plots. Calculation of carbon stocks in the litter layer and in soil organic matter followed the description given in section 5.4.1. Aboveground carbon stock in each forest type was determined by applying the allometric models selected from the literature (Table 3). Diameter at breast height data, collected from the forestry inventories, were also used as the dependent variable to determine aboveground biomass, and hence carbon stocks.

For mountain miombo forest, belowground biomass was calculated using a conversion rate (root to shoot ratio) of 0.48, as the mid-point of the max-min range of 0.40-0.56 found in the miombo literature (Mokany et al., 2006, Ryan et al., 2011, Chidumayo, 2013, Mugasha et al., 2013, Kachamba et al., 2016). For the non-native species, *i.e. P. taeda* and *E. grandis*, belowground biomass was calculated using a regression function (Equation 2) suggested by Cairns et al. (1997), which estimates belowground biomass as a function of aboveground biomass. It reflects the age of forest plantations, and no distinction is made between species of *Pinus* (Gymnosperm) and *Eucalyptus* (Angiosperm) growing in tropical zones:

$$BGB = Exp\left(1.3267 + 0.8877 * Ln(AGB) + 0.1045 * Ln(A)\right) \qquad \text{(Eq. 2.)}$$

where BGB (Mg ha^{-1}) is belowground biomass stock (coarse roots), AGB (Mg ha^{-1}) is stock of living biomass of trees above ground (*i.e.* stems, branches and foliage) and A is the average age, which in this thesis was taken as 34 years during the assessment year 2012.

5.4.3 Net ecosystem production (**Paper II**)

Net ecosystem production was calculated for the *P. taeda* and *E. grandis* plantations, based on the assumption that carbon stocks in miombo soils and biomass had been in approximately steady state since the time of establishment of the plantations, and could thus be used as reference. Net ecosystem production (Mg ha^{-1} yr^{-1}) was thus calculated as the difference in total carbon stocks between plantation and miombo stands divided by 34, the age of the plantation stands.

5.4.4 Net primary production (**Paper III**)

Net primary production

Net primary production (NPP) was calculated as the sum of incremental amount of carbon in biomass and carbon lost in foliar and fine-root biomass, *i.e.* the litter production in short-lived biomass components. Net primary production allocated to foliage was thus accounted for both as losses in litterfall and as the increment in foliage biomass, included as an unspecific part of the allometric functions(Clark et al., 2001a). In practice, NPP was determined based on Equation 3, which includes four components:

$$NPP = CL_L + CI_A + CI_{CR} + CI_{FR} \qquad \text{(Eq. 3.)}$$

where CI_L (Mg ha^{-1} year^{-1}) is annual carbon in litterfall, mostly foliar litter, CI_A (Mg ha^{-1} year^{-1}) is annual aboveground carbon increment, CI_{CR} (Mg ha^{-1} year^{-1}) is annual belowground carbon increment (coarse roots) and CI_{FR} (Mg ha^{-1} year^{-1}) is annual fine root production.

Aboveground and belowground carbon increment

Aboveground and belowground carbon increment (Mg ha^{-1} yr^{-1}) were determined directly by calculating the difference in aboveground carbon stocks (Mg ha^{-1}) between the two sampling periods, divided by the sampling period (16 months expressed in years). The biomass stocks, *i.e.* carbon stocks for each compartment and forest type, were determined following the same procedures as described earlier for calculation of total carbon stocks.

Thus, aboveground biomass stock was calculated by applying the allometric models in Table 3, depending on forest type. For belowground biomass stocks, a conversion factor of 0.48 (root-to shoot-ratio) and a regression function (Equation 2) were used for the calculations for miombo and non-native species, respectively.

Fine root production and turnover rate

Fine root increment (Mg ha^{-1} $year^{-1}$ of biomass) was estimated per forest type by summing the biomass (Mg ha^{-1}) produced on the two sampling occasions and dividing by the sampling period (15 months) expressed in years. Biomass was also converted to carbon assuming a 50% carbon content (Grace et al., 2006). The residence time of the biomass (years), a measure of fine root longevity, was calculated from the ratio of initial fine root biomass to annual fine root production. Dead and live roots were not possible to separate in a systematic matter, which can probably add to an underestimation of fine root production in this thesis work.

Carbon in litterfall

The total annual litterfall was also calculated for each forest type and as the average of the material collected from the three plots sampled during the study interval. At plot level, however, the annual litterfall (Mg ha^{-1} $year^{-1}$) was estimated by dividing the whole biomass (Mg ha^{-1}), obtained from the 15 litter traps, by the sampling period (12 months) expressed in years.

5.4.5 Leaf litter decomposition rate (**Paper IV**)

Decomposition rate for the five substrates in litter decomposition experiments, was determined using two different decomposition models, namely: a simple first-order exponential decomposition model (denoted K-model hereafter), which assumes a constant decomposition rate of a substrate over time (Olson, 1963), and Q-model, which is based on the concept of continuously decreasing litter decomposability (decomposition rate) (Ågren and Bosatta, 1998).

5.5 Statistical analysis

In **Papers I** and **II**, the linear mixed-effects model in the ‘lme4’ package (Bates et al., 2015) was used to perform the statistical analysis, to better account for differences between tree species effects, and not between study sites. The model was run with the study sites (Inhamacari, Penhalonga and Rotanda) treated as random effect and forest types as fixed effects. Total ecosystem carbon stocks and its components (Table 1), soil pH and soil nutrients (*i.e.* nitrogen and phosphorus) were the dependent variables tested. Two-way analysis of variance (α=0.05) was used to evaluate the changes driven by the *P. taeda* and *E. grandis* plantations in the parameters studied. In **Paper III**, one-way analysis of variance was used to check for statistically significant differences in the mean across the three forest types (mountain miombo, *P. taeda* and *E. cloeziana*) with respect to net primary production and its components (Table 1).

In **Papers I, II** and **III**, pair-wise comparisons between the forest types were based on Tukey's post hoc test (α=0.05), with P-value (p) adjusted using the single-step method (Hothorn et al., 2008). The probability values (p) were determined using the 'multcomp' package (Hothorn et al., 2015). Pearson product-moment correlation (r) analysis was used to measure the strength of associations and the direction of the relationship between selected parameters.

In **Paper V**, the allometric equations were constructed for lowland miombo forest, and the fitting was performed using the non-linear least squares approach in the package 'nlstools' (Baty et al., 2015). All statistical analyses and tests performed in Papers **I, II, III** and **V** were carried out using R statistical software, version 3.1.2 (RCoreTeam, 2014).

In **Paper IV**, mass loss data for the five substrates were fitted to two different decomposition models, a simple first-order exponential decomposition model (denoted K-model hereafter) and Q-model, to predict the long-term effects of foliage litter decomposition of *Pinus taeda*, *Eucalyptus cloeziana* and deciduous miombo trees on soil carbon stocks. Since litter decomposition rates were only studied here for each litter type in its respective stand, it was not possible to directly distinguish the influence of substrate quality from that of possible differences in site conditions such as soil temperature, which is an important determinant of microbial growth rate. To distinguish between these two components, the statistical methods were used, by setting values for initial substrate quality and microbial growth rate separately in the Q-model. Parameters setting of the Q-model was performed separately for each litter type, using the NLMIXED procedure for SAS/STAT software, Version 9.4 (SAS, 2013).

6 Results

6.1 Soil carbon, nutrients, and acidity (**Paper I**)

The *Pinus taeda* and *Eucalyptus grandis* plantations had higher total soil organic carbon content (0-50 cm) than mountain miombo forest, which supported the first hypothesis tested in this thesis (**H1)**, but there was no marked difference between the pine and eucalyptus stands in this regard. This partly contradicted hypothesis **H2**, that the effect of *E. grandis* is stronger than that of *P. taeda*. Thus, the stock of soil organic carbon for the whole soil profile (0-50 cm) was 55% larger in *P. taeda* ($p<0.05$) and 60% larger in *E. grandis* ($p<0.05$) than in adjacent mountain miombo (87 Mg ha^{-1}) (Figure 6a, Table 5). Total stock of soil organic carbon did not differ significantly between the planted forests ($p>0.1$). The plantation of *E. grandis* had a significant effect on carbon stocks in both the organic horizon (0-10 cm) and the mineral soil (30-50 cm). Litter layer carbon was 60% and 79% lower in miombo forest (2.6 Mg ha^{-1}) than in plantations of *E. grandis* and *P. taeda*, respectively ($p\leq0.001$) (Figure 6a, Table 5).

There was a weaker ($p>0.1$) effect of the *P. taeda* and *E. grandis* plantations on total soil nitrogen stocks (0-50 cm layer) (Figure 6b) than that found for soil organic carbon stocks (Figure 6a), but hypothesis **H1** was still largely supported. Total stocks of soil nitrogen ranged from 5.9 Mg ha^{-1} in miombo forest to 7.0 Mg ha^{-1} in *E. grandis*, with *P. taeda* intermediate (6.7 Mg ha^{-1}).

Soils under plantations of *E. grandis* had elevated soil pH and reduced extractable soil phosphorus. The soils in *E. grandis* stands were significantly less acidic than those in the other two stand types, which were characterised as only weakly or moderately acid. In *E. grandis* stands, soil pH in the 10-30 cm layer ($p=0.05$) and 30-50 cm layer ($p<0.05$) was 0.6 and 0.8 pH units higher, respectively, than in miombo forest. Extractable phosphorus stocks (Figure 6c) were 22% lower in *E. grandis* soils (0-50 cm) than in miombo forest soils

($p<0.01$). Miombo and *P. taeda* soils did not differ significantly with respect to extractable phosphorus stocks. Extractable phosphorus stocks in *E. grandis* soil were also significantly lower than in *P. taeda* soil ($p<0.001$). In both the *E. grandis* and *P. taeda* plantations, extractable phosphorus and soil organic carbon were strongly ($p<0.001$) and positively correlated to each other (Pearson's r = 0.97). These results contradicted hypothesis **H3**, which stated that decreased stocks of extractable phosphorus are a consequence of increased nutrient demand and uptake in trees. The results also contradicted hypothesis **H4**, which stated that soil acidification increases as a consequence of increased stocks of soil carbon and nutrient accumulation in biomass.

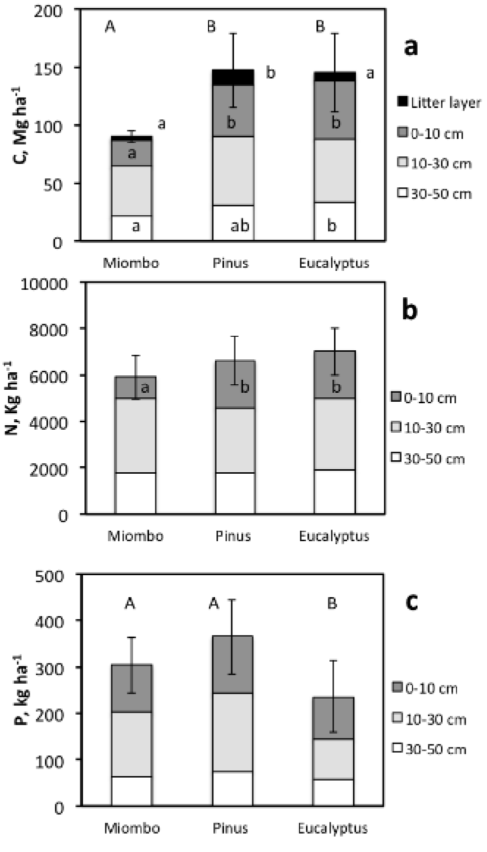

Figure 6. Mean stocks of a) soil carbon (C), b) total soil nitrogen (N) and c) extractable phosphorus (P) in the three forest types studied and across soil layers. The error bars indicate standard deviation of the mean for the whole soil profile. Different lower-case and upper-case letters indicate significant difference for individual soil layers and for the whole soil profile, respectively, between forest types ($p<0.05$). N and P in the litter layer were not determined.

6.2 Total ecosystem carbon stocks (**Paper II**)

Total ecosystem carbon stocks (soil, litter layer and tree biomass) in 34-year-old plantations of *Pinus taeda* and *Eucalyptus grandis* (Table 5) were significantly greater than corresponding carbon stocks in adjacent mountain miombo in the Western highlands of Manica province, within the Beira corridor study area in Mozambique. The total ecosystem carbon stocks were around two-fold higher in both *P. taeda* and *E. grandis* plantations than in mountain miombo ($p<0.01$) (Table 5).

The carbon stocks in aboveground biomass of *P. taeda* and *E. grandis* were in proportion to previously measured differences in soil organic carbon stocks involving the same forest types used as reference (**Paper I)**, and were greater than the corresponding carbon stocks in miombo sites, which supported hypothesis **H5**. Thus, aboveground carbon stocks were around eight-fold and 10-fold higher in the plantations of *P. taeda* ($p<0.05$) and *E. grandis* ($p<0.01$) than in miombo forest stands, which had estimated stocks of 17.9 Mg ha^{-1}.

Aboveground carbon stocks did not differ significantly between the two plantation species (Table 5), although the stock of carbon in *E. grandis* plantation was 25% higher than in *P. taeda* plantation. Belowground biomass, which was calculated from aboveground biomass, followed a similar trend to that of aboveground biomass and also decreased in the order: *Eucalyptus*> *Pinus*>> miombo (Table 5).

Table 5. *Average (± standard deviation) carbon (C) stocks per carbon pool, and total ecosystem stocks of each forest type studied at the Inhamacari, Penhalonga and Rotanda forest sites in the Western highlands of Manica province, Mozambique. Different letters within lines indicate significant differences between forest types ($p<0.05$).*

Compartment (Mg ha^{-1})	Forest type		
	Mountain miombo	*P. taeda*	*E. grandis*
Soil organic carbon stocks	87.3 ^{a} (± 8.6)	135.2 ^{b} (± 51.1)	138.8 ^{b} (± 60.2)
Aboveground carbon stocks	17.9. ^{a} (± 3.6)	162.1 ^{b} (± 64.0)	202.5 ^{b} (± 124.6)
Belowground carbon stocks	8.6 ^{a} (± 1.8)	53.3 ^{b} (± 17.7)	58.7 ^{b} (± 31.0)
Litter layer carbon stocks	2.6 ^{a} (± 1.0)	12.1 ^{b} (± 5.6)	6.6 ^{ab} (± 3.1)
Total ecosystem carbon stocks	116.4 ^{a} (± 11.1)	362.7 ^{b} (± 136.9)	406.6 ^{b} (± 204.2)

Hypothesis **H6**, which stated that aboveground carbon stocks in plantation biomass comprise a greater proportion of total ecosystem carbon stocks than in miombo biomass, was also supported by the results (Figure 7). This hypothesis was based partly on Figure 4. Analysis of the relative distribution of carbon in different compartments revealed that soil carbon and litter carbon were the most important components of total carbon stocks in miombo forest (Figure 7), amounting to 75% of total ecosystem carbon stocks. In contrast, in the plantations of *P. taeda* and *E. grandis* aboveground carbon stocks were the major carbon pool, accounting for 45% and 50% of the total estimated carbon stocks, respectively.

6.3 Net ecosystem production (**Paper II**)

We described that carbon stocks in miombo were used as the carbon baseline for estimating carbon sequestration at the ecosystem scale, *i.e.* net ecosystem production in the plantation stands. The *P. taeda* and *E. grandis* plantations had similar performance with respect to total ecosystem carbon stocks (Table *5*) and net ecosystem production (Table *6*).

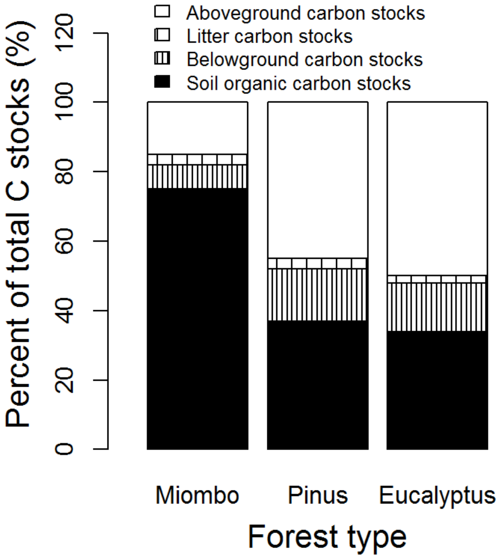

Figure 7. Relative distribution of carbon (C) stocks in the different compartments that represent total ecosystem carbon stocks in mountain miombo and in *Pinus taeda* and *Eucalyptus grandis* plantations at the Inhamacari, Penhalonga and Rotanda forest sites in the Western highlands of Manica province, Mozambique.

Table 6. *Mean annual accumulation of carbon in* Pinus taeda *and* Eucalyptus grandis *biomass. The calculations assumed miombo forest as reference and stand age of the planted forests species was 34 years.*

ID	Compartment (Mg ha^{-1} yr^{-1})	*P. taeda*	*E. grandis*
1	Aboveground biomass	4.24	5.43
2	Belowground biomass	1.31	1.47
3	Soil 0-50 cm depth	1.41	1.51
4	Litter layer	0.28	0.12
5	Biomass sum (1+2)	5.56	6.90
6	Soil and litter sum (3+4)	1.69	1.63
7	Net ecosystem production (5+6)	7.24	8.54

The average net ecosystem production in *P. taeda* and *E. grandis* biomass and soil was 7.24 and 8.54 Mg C ha^{-1} $year^{-1}$, respectively, assuming mountain miombo as reference and 34 years as the age of the planted species (Table 6). Thus carbon increment in biomass (aboveground + belowground) was the dominant part of net ecosystem production (*i.e.* 81% in *E. grandis* and 77% in *P. taeda*) (Table 6). This increment was also reflected in higher ratio between biomass carbon and soil carbon stocks in the two plantation species compared with mountain miombo.

6.4 Net primary production (**Paper III**)

It should be borne in mind that net primary production was determined in plantations of *E. cloeziana*, not the *E. grandis* plantations referred to in previous sections. This change of *Eucalyptus* species was in order to meet the criteria established to select non-native species for three plots per forest type. At Inhamacari, the plantation of *E. cloeziana* fulfilled the selection criteria, but the *E. grandis* plantation did not. Overall, the carbon stocks in the litter layer of *E. grandis* (6.6 Mg ha^{-1}) and *E. cloeziana* (13.9 Mg ha^{-1}) stands in Inhamacari were very similar, but soil organic carbon stocks were much lower in the study plot with *E. cloeziana* (47.7 Mg ha^{-1}) compared with *E. grandis* (138.8 Mg ha^{-1}).

The findings obtained supported hypothesis **H7,** that net primary production is higher in *P. taeda* and *E. cloeziana* plantations than in mountain miombo (Table 7). In fact, net primary production was three-fold higher in *E. cloeziana* plantations ($p<0.001$), and two-fold higher in *P. taeda* plantations ($p<0.001$) than in mountain miombo (Table 7). Comparing the planted forests, the *E. cloeziana* plantations showed a higher level of net primary production (Table 7). Net primary production also showed a strong positive correlation with basal area across forest types (Figure 8), confirming hypothesis **H8**.

Table 7. *Average values of net primary production and its components (± standard deviation) depending on forest type.*

Parameter ($Mg·ha^{-1}·year^{-1}$)	Forest type Mountain miombo	 *P. taeda*	 *E. cloeziana*
Net primary production	5.12^a (± 1.41)	14.10^b (± 0.32)	19.88^c (± 0.79)
Carbon in litterfall	2.30^a (± 1.15)	4.64^b (± 0.45)	4.78^b (± 0.78)
Aboveground carbon increment	1.55^a (± 0.37)	6.39^b (± 0.15)	10.35^c (± 0.49)
Belowground carbon increment (excl. fine roots)	0.74^a (± 0.00)	2.24^b (±0.05)	3.83^c (± 0.18)
Fine root production	0.53^a (± 0.07)	0.83^b (± 0.11)	0.92^b (± 0.13)

Different letters within lines indicate significant differences between the forest types ($p<0.05$).

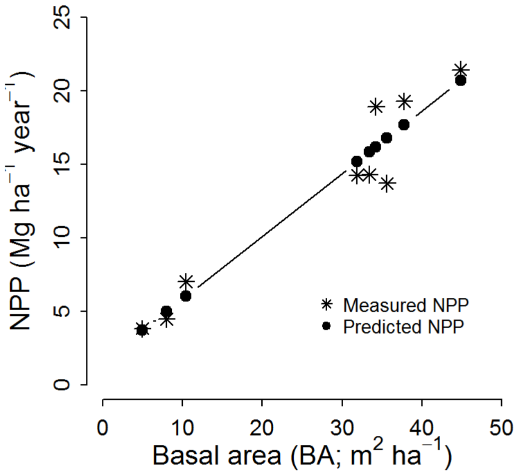

Figure 8. Linear relationship between basal area (BA) and net primary production (NPP) in forest at the Inhamacari study site in Mozambique, regardless of forest type (miombo forest, *Pinus taeda* and *Eucalyptus cloeziana*). NPP = 0.426 x (BA) +1.607, t-test = 9.538, P<0.0001, adjusted R-squared= 92%, standard error = 1.87.

On the other hand, hypothesis **H9** was rejected, since there were pronounced differences in carbon allocation between mountain miombo and the non-native tree species. The largest proportion of net primary production in *Eucalyptus*, in particular, and in *Pinus* stands was allocated to aboveground biomass increment, whereas in miombo stands, the largest part of net primary production was allocated to litterfall (Figure 9). Thus, the contribution of aboveground carbon increment to total net primary production was about 52% in *E. cloeziana* and 45% in *P. taeda* (Figure 9). In contrast, in mountain miombo, litterfall was the most important component, accounting for 43% of the total measured net primary production.

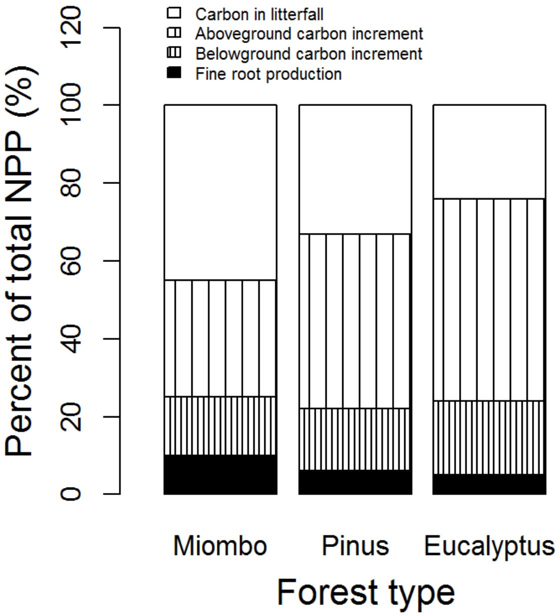

Figure 9. Partitioning of total net primary production (NPP) among the four carbon compartments studied in the different types of forest. In mountain miombo, the largest fraction of total NPP was carbon in litterfall (45% of total). In *Pinus taeda* and *Eucalyptus cloeziana* plantations, the largest fraction was aboveground carbon increment (45% and 52% of total NPP, respectively).

Increment in aboveground biomass was about three-fold larger *in P. taeda* plantation ($p<0.0001$) and six-fold larger in plantation of *E. cloeziana* ($p<0.0001$) than in miombo forest (Table 7). Annual rate of litterfall was approximately two-fold higher in *Pinus* and *Eucalyptus* plantations than in miombo forest (Table 7). This difference was statistically significant ($p<0.04$ in both cases), but there was no statistically significant difference between the *Pinus* and *Eucalyptus* plantations ($p>0.1$).

Across all forest types, fine root production was largely proportional to other components of net primary production, in particular litterfall (Figure 9). Fine-root production was 74% higher ($p<0.01$) in stands of *E. cloeziana* and 57% higher ($p=0.03$) in *P. taeda* stands than in mountain miombo (Table 7). Fine root turnover rate decreased in the order *Eucalyptus* (0.98 Mg ha^{-1} year^{-1}) > *Pinus* (0.87 Mg ha^{-1} year^{-1}) > miombo (0.53 Mg ha^{-1} year^{-1}). These rates imply that the longevity of fine roots, *i.e.* residence time, was about 2 years in miombo forest stands and 1 year in *Pinus* and *Eucalyptus* stands. The difference in fine root turnover between miombo and *E. cloeziana* was significant ($p=0.03$).

6.5 Changes in stem diameter (DBH) growth (**Paper III**)

Increment in DBH ranged from 0.48 cm year^{-1} in mountain miombo forest to 0.97 cm year^{-1} in *Eucalyptus cloeziana* plantation, with *Pinus taeda* intermediate (0.66 cm year^{-1}). The increment was significantly greater (102%) in *E. cloeziana* stands than miombo ($p<0.001$). The DBH increment in *P. taeda* plantation was around 37% higher than at miombo sites, but this difference was not statistically significant ($p>0.1$).

6.6 Leaf litter decomposition study (**Paper IV**)

6.6.1 Leaf litter decomposition rate

At the end of the one-year decomposition study, about half or less of the initial mass remained. Hypothesis **H10**, that decomposition rate of miombo foliar litter is more rapid than that of *P. taeda* and *E. cloeziana* litter, was supported by the findings. The K-model results revealed that the mean decomposition rate constant (k) was highest for *Brachystegia spiciformis* (0.818), followed by mixed miombo litter (0.65), *Uapaca kirkiana* (0.583), *E. cloeziana* (0.535) and *P. taeda* (0.433) litter. The higher value of k for litter of the two dominant miombo species *B. spiciformis* and *U. kirkiana* and the six-species mixed miombo litter indicated that the deciduous litter in miombo stands generally decomposed faster than the evergreen *E. cloeziana* and *P. taeda* litters. In agreement with values obtained with K-model, the Q-model results indicated that the decomposition rate was highest for *B. spiciformis* litter in the miombo stand (0.524), followed by the *E. cloeziana* (0.399) and *P. taeda* (0.351) litters. This difference between *Brachystegia* litter in miombo forest and *P. taeda/E. cloeziana* litter was statistically significant ($p<0.0001$ in both cases).

Hypothesis **H11**, which stated that the decomposition rate is determined primarily by differences in substrate quality, was not supported. The Q-model results indicated that differences in decomposition rate between litter types were best explained by differences in microbial growth rate, whereas differences in initial litter quality had no significant impact (**Paper IV**).

6.6.2 Long-term carbon accumulation rate

The predicted long-term consequences of the measured litterfall rates and decomposition rates described by the K- and Q-models are shown in *Figure 10* for two periods, 34 years (the approximate age of the *P. taeda* and *E. cloeziana* stands at the time of this study) and steady-state carbon accumulation.

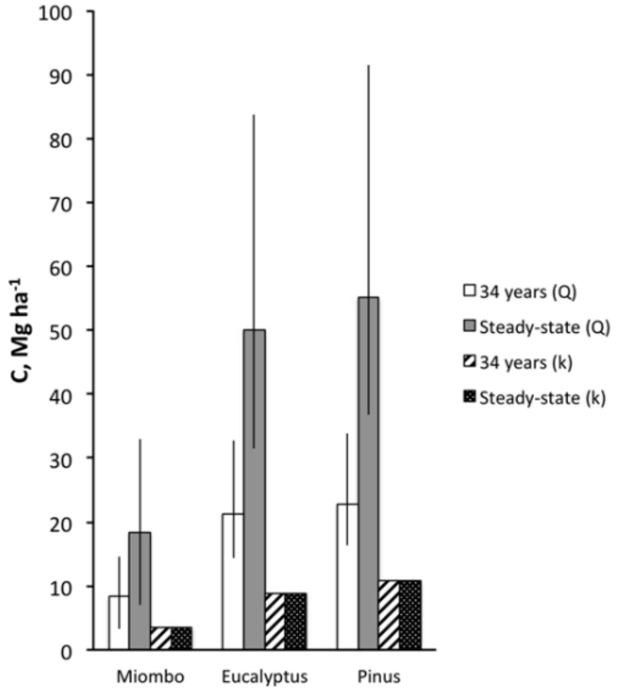

Figure 10. Predicted accumulated carbon (C) stocks (Mg ha^{-1}) in different forest types after 34 years and at steady state, according to two decomposition models: Q-model (Q) and K-model (K). Annual litter input was assumed to be equal to measured rate of litterfall. Mean carbon stocks were calculated with the best estimate for the decomposer growth rate in the Q-model. Error bars show the range of carbon accumulation resulting from using different values of the decomposer growth rate, *i.e.* the 95% confidence limits in estimating decomposer growth rate.

Hypothesis **H12**, that measured carbon stocks in the litter layer are explained by observed litterfall and litter decomposition rate over a 34-year stand rotation, was partly supported by the model predictions of higher carbon accumulation in the litter layer in *P. taeda* and *E. cloeziana* stands than in mountain miombo. The hypothesis was also supported for the pine stands, since the 34-year prediction was reasonably accurate for the litter layer in those stands. However, the hypothesis was not supported for the other forest types, since predictions overestimated litter carbon stocks, particularly in miombo forest.

The accumulated carbon stocks in the K-model were the same for the 34-year prediction and at steady-state. Compared with measured carbon stocks in the litter layer, predicted accumulated carbon stocks were similar in miombo, lower in *E. cloeziana* and much lower in *P. taeda* stands. By contrast, the Q-model predicted much larger carbon stocks. The accumulated carbon stocks after 34 years were less than half those at steady state for all forest types. Predicted carbon accumulation rates in miombo were also less than half the accumulation rates in *P. taeda* and *E. cloeziana* stands (Figure 10). Predictions accounting for the confidence limits in estimating decomposer growth rate resulted in a large range in carbon stocks.

The predicted carbon stocks showed the same ranking of forest types as found for observed carbon stocks in the litter layer. The mean value of predicted carbon accumulation rate after 34 years was similar to measured carbon stocks in the litter layer of the *P. taeda* stands (83%), but was higher, or much higher, than observed stocks in stands of *E. cloeziana* (65%) and miombo (39%). The observed carbon stocks in the litter layer fell within the confidence limits of predicted carbon stocks for *P. taeda*, but in the *E. cloeziana* and miombo stands measured carbon stocks were outside the confidence limit of predictions.

Mean predicted steady-state carbon accumulation was markedly greater than observed in the litter layer for all stands, but was smaller than the total observed carbon stocks in the litter layer and 0-50 cm soil layer (Figure 10). Mean predicted steady-state carbon stocks derived from aboveground leaf litter represented 23, 81 and 42 % of the observed total soil and litter stocks in mountain miombo, *E. cloeziana* and *P. taeda* stands, respectively.

6.7 Biomass equations for lowland miombo (**Paper V**)

Two interchangeable biomass equations (Figure 11) were developed in this thesis for estimating total aboveground biomass (stem, branches and foliage) of multi-species lowland miombo in the Beira corridor study area in Mozambique, based on stem diameter at breast height (DBH) and stump diameter (SDI). The predictive accuracy of the DBH-based equation was as follows: precision (*i.e.* adjusted R-squared) between 98-99%, average bias between 0-0.1 kg per individual and root mean square error between approximately 30-69 kg per individual. For the SDI-based equation, the predictive accuracy was: precision between 86-96%, average bias between 0-0.8 kg per individual and root mean square error between approximately 70-101 kg per individual.

The degree of precision and reliability of these equations was high within the limits of the Beira corridor study area. The SDI-based equation is principally intended for estimation of carbon stocks in harvested trees, and thus for reconstructing the former carbon stocks in forests subjected to logging. The DBH-based equation is recommended for estimating carbon stocks of live trees, due its better precision compared with the SDI-based equation. Additional verification of the adequacy of the two new biomass equations developed was made by comparing with other biomass equations obtained from the literature (Brown, 1997, Chamshama et al., 2004, Ryan et al., 2011, Chidumayo, 2013, Mugasha et al., 2013, Kuyah et al., 2014, Kachamba et al., 2016) (Figure 12). The equation developed in this thesis produced the best predictions, but the DBH-based equation by Mugasha et al. (2013) (Figure 12A) and the SDI-based equation by Chamshama et al. (2004) (Figure 12B) also gave good estimates (low relative bias) for lowland miombo forest of the Beira corridor study area.

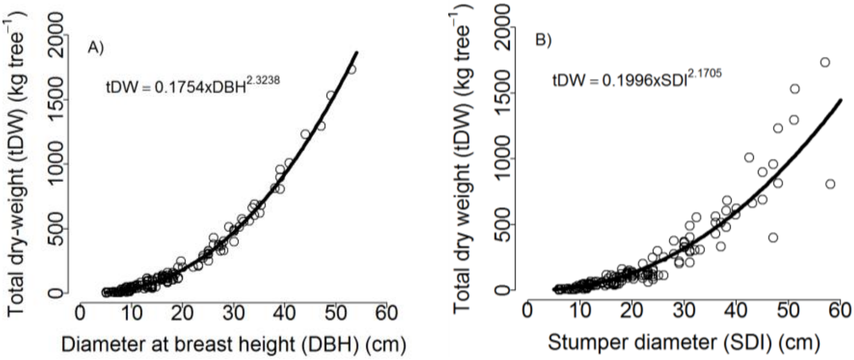

Figure 11. Fitted line for the relationship between total dry weight (stems, branches and foliage) and a) diameter at breast height and b) stump diameter.

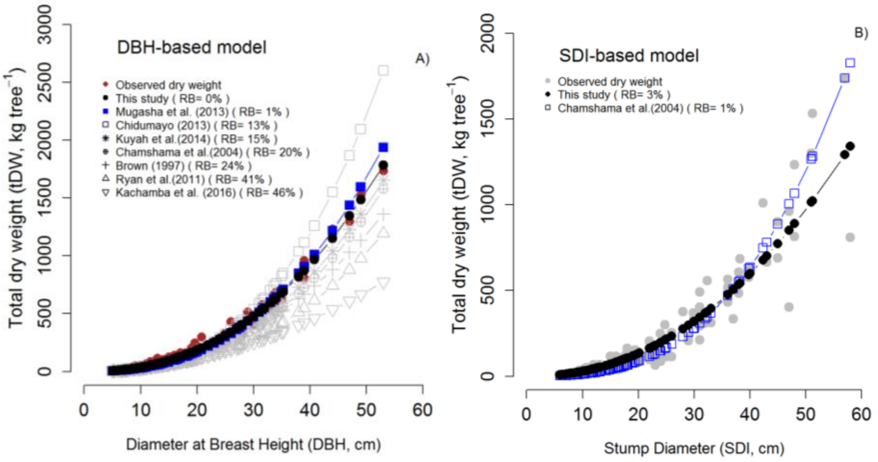

Figure 12. Visualisation of the predictive accuracy of the diameter at breast height (DBH)-based model developed in this study verses that of DBH-based models selected from the literature compared with total dry weight (stem, branches, and foliage) of sampled trees from the construction dataset (A); and the stump diameter (SDI)-based model developed in this study verses that of the SDI-based model found in the literature (Chamshama et al., 2004) compared also with total dry weight (stem, branches, and foliage) of sampled trees from the construction dataset (B).

Use of both the DBH- and SDI-based equation developed in this thesis work should be restricted to lowland miombo type of the Beira corridor study area, not mountain miombo. As shown in Figure 13, the tree allometry of these two subtypes of miombo differs significantly, as can also be seen in Figure 3.

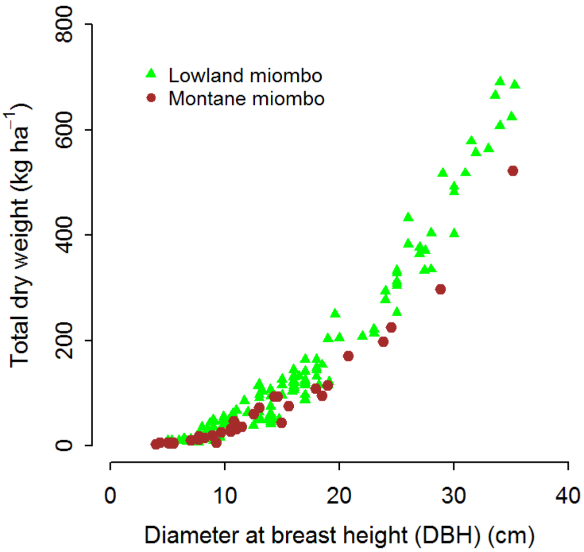

Figure 13. Scatter plot showing the relationship between diameter at breast height (DBH) and total dry weight (stem, branches and foliage) in lowland miombo (<1100 m a.s.l.) and miombo forest (1100-1700 m a.s.l.) in the Beira corridor study area, Mozambique. For the same DBH size, total dry weight of individual trees was significantly lower in mountain miombo (t-test = 36.84; $p<0.0001$), suggesting that the allometry of these two miombo types differs. No trees with DBH >40 cm were found in the mountain miombo landscape, so trees with similar DBH sizes to the lowland miombo type were used to perform this comparison.

7 Discussion

Miombo forest and plantations of *Pinus* and *Eucalyptus* species occur in various climate and soil conditions in southern Africa. The work presented in this thesis was conducted in the Beira development corridor of central Mozambique. This region includes the Western highlands of Manica province, where the studies described in **Papers I-IV** were conducted, and lowland areas, where the study described in **Paper V** was conducted. The regional context was considered important in this thesis, since new knowledge with relevance for specific regions in Mozambique is required to guide reforestation programmes (Coetzee and Alves, 2005, MINAG, 2009).

The Western highlands of Manica province are characterised by a mountain miombo type that is structurally different from the lowland miombo type (Figure 3). In particular, the lowland miombo is characterised by higher stem density and taller trees than the mountain miombo (Sitoe, 2005). Actually, seven different types of miombo forests have been distinguished in Mozambique, based on physiognomy and structure (MINED, 1986).

The plantation stands studied in **Paper I-IV** were the first rotations of these species at the study site, and they were also among the first large-scale industrial plantations in Mozambique. At 34 years of age, the stands had grown larger and higher than would normally be the case for optimum forest management, where stand rotations take normally 20 years. However, time is an important factor in studies of tree species effects on soils. As indicated by Li et al. (2012), it takes about three decades to see the effect of pine and eucalypt plantations on soil organic carbon stocks in abandoned farmland, and about 50 years to discern significant effects on total nitrogen stocks in soils. Thus, the study sites provided a unique opportunity in Mozambique to quantify the influence of a first and single forest rotation of fast-growing trees that was sufficiently long to make it likely to reveal tree species effects on the soil.

The results obtained supported many of the hypotheses tested. For example, the *Pinus* and *Eucalyptus* plantation accumulated much higher aboveground biomass than was observed in adjacent mountain miombo and there were also higher total carbon and nitrogen stocks in the soil and the litter layer, including belowground biomass. Furthermore, net primary production was significantly greater in the plantations than in the native miombo. The higher soil stocks of carbon and nitrogen could be explained to some extent by higher leaf litterfall, from the predictions with Q-model. However, the model predictions neglected root litter, due to lack of empirical data (root production was observed only in the surficial soil layer, and data on decomposition of roots were lacking). Higher root litter production in plantation stands was therefore probably an additional, and important, contributor to the higher soil organic carbon stocks after a 34-year full rotation.

It is also important to point out some features of the studies that probably introduced uncertainties into the measurements, estimates and conclusions presented in this thesis. The study design in **Papers I** and **II**, which included miombo, *Pinus taeda* and *Eucalyptus grandis*, involved three study sites located about 100-200 km apart near the Zimbabwe border. This design made it possible to apply a randomised block design to test tree species effects at the regional scale. However, the process-orientated studies in **Papers III** and **IV** could only be performed at the Inhamacari site, for many practical reasons. It was also decided to replace *E. grandis* with stands of *E. cloeziana*, since only the latter stands met all the initial criteria for selecting forest stands (see Section 5.2). The statistical design of the studies presented in **Papers III** and **IV** was thus not as strong as that in **Papers I** and **II**. In particular, the selection of another species of *Eucalyptus* was an important difference that should be borne in mind when considering tree species effects.

Eucalyptus cloeziana and *E. grandis* have very similar branch and leaf morphology. Tests of the allometric functions (**Paper II**), which included both species, indicated that the same equation can be used to predict total aboveground biomass from diameter at breast height (DBH> 5 cm) for both species. However, a distinct difference between the two species is that the bark of *E. cloeziana* is rugged, thick and similar to pine bark, whereas *E. grandis* has smooth bark and long strips of the outer bark continually peel off the stem. Bark litter is therefore an important additional litter type in *E. grandis* forests, in addition to leaf litter, whereas it is lacking in *E. cloeziana* stands. Another difference is that *E. grandis* stands often have an understorey of young saplings, whereas stands of *E. cloeziana*, and *P. taeda*, have virtually no understorey layer.

Another possible source of uncertainty is the use of miombo forest as the carbon baseline in **Papers I** and **II,** where the current carbon status in miombo stands was assumed to represent steady-state conditions. However, there is a lack of documentation on previous states of these miombo forests to firmly validate this assumption. Similarly, it can be argued that the measurements of stem diameter increment, litterfall and fine root production would have be less uncertain and more representative if they had been made over longer periods of time. These uncertainties can only be tested from alternative calculations of carbon dynamics.

One feature of the experimental data that appears to corroborate the results obtained in this thesis is that the estimates of biomass, production of biomass and litter and estimated soil changes were mostly of the same order of magnitude and range as reported previously in other similar studies. There is of course an obvious danger in using the results of previous studies as a validation of observations, since new and very different estimates can sometimes be more accurate than previous findings. Another way to validate the accuracy of the estimates is by using the equation:

$$\text{NEP} = \text{NPP} - \text{Resp}_H \qquad \text{(Eq. 4.)}$$

where NEP (Mg ha^{-1} yr^{-1}) is net ecosystem production, NPP (Mg ha^{-1} yr^{-1}) is net primary production, and $Resp_H$ (Mg ha^{-1} yr^{-1}) is heterotrophic respiration.

In **Paper II**, net ecosystem production was calculated for the plantation species at the three sites using miombo as a carbon baseline and the results indicated continuous long-term change. In **Paper III**, net primary production was estimated for all three forest types at one of the sites, Inhamacari, and by using short-term measurements. The heterotrophic respiration that originated from leaf litter can be roughly estimated from data in **Paper IV**, by subtracting predicted cumulative carbon stocks in the remaining mass of leaf litter from the total cumulated carbon in leaf litterfall after 34 years. The results of this comparison are shown in Table 8.

The net ecosystem production estimate for *P. taeda* based on total ecosystem carbon stocks and using miombo as a baseline was 7.2 Mg ha^{-1} yr^{-1}, which is lower than the value estimated from net primary production minus leaf litter respiration (10.1 Mg ha^{-1} yr^{-1}). The discrepancy between the values was expected and would more or less disappear if root litter were included in the decomposition data in **Paper IV**, as an additional source of heterotrophic respiration. The net ecosystem production estimate for *E. grandis* (8.5 Mg ha^{-1} yr^{-1}) was almost half that for *E. cloeziana* (15.7 Mg ha^{-1} yr^{-1}) based on net primary production and leaf litter respiration. Underestimation of heterotrophic respiration can partly explain the difference, but there are probably also other causes of the differences between the *Eucalyptus* species.

Table 8. *Comparison of net primary production (NPP), net ecosystem production (NEP) and heterotrophic respiration ($Resp_H$) at the Inhamacari, Penhalonga and Rotanda forest sites in the Western highlands of Manica province, Mozambique. The calculations of NEP assumed miombo forest as reference and stand age of the planted forests species was 34 years.*

Forest type	Paper III	Paper IV	Paper III+IV	Paper II
	NPP ($Mg\ ha^{-1}\ yr^{-1}$)	$Resp_H$ ($Mg\ ha^{-1}\ yr^{-1}$)	NEP ($Mg\ ha^{-1}\ yr^{-1}$)	NEP ($Mg\ ha^{-1}\ yr^{-1}$)
Mountain miombo	5.12	2.1	n.d.	n.d.
Pinus taeda	14.1	4	10.1	7.2
E. grandis	n.d.	n.d.	n.d	8.5
E. cloeziana	19.9	4.2	15.7	n.d.

In conclusion, cross-estimation of net ecosystem production for *P. taeda* and the two *Eucalyptus* stands indicated that the estimates were reasonably accurate. Moreover, a comparison performed with relevant studies on net ecosystem production (Kinerson et al., 1977, Sampson et al., 2008, Cabral et al., 2011) and net primary production (Murphy, 1975, Kinerson et al., 1977, Sampson et al., 2008), indicated that our estimates were within expected ranges, for both forest types.

The studies in **Papers I-IV** examined only the first-rotation effects of pine and eucalypt plantations. There was markedly higher productivity in these stands, despite the lack of fertiliser application over the years, compared with that in mountain miombo. Furthermore, the pine and eucalypt plantations increased the carbon and nitrogen concentrations in the topsoil, but the nitrogen and phosphorus concentrations in tree biomass of the plantation trees were probably also much higher. The latter finding indicates that repeated rotations of pine and eucalyptus may cause nutrient depletion in soils and, unless compensatory nutrients are applied, this will decrease plantation forest productivity over time.

In fact, signs of nutrient depletion were evident in the mature plantations of *E. grandis* in the study area. This observation is in line with previous claims that productivity declines in monoculture plantations of fast-growing trees due to their high nutrient demand (Lamb, 2011). Thus, the role of nutrients in maintaining the long-term productivity of both plantation and natural forests in this region is an important question for future research. This includes a better understanding of natural processes in nutrient cycles and the effect of compensatory nutrient application in the form of fertiliser.

Since allometric biomass equations are essential tools for estimating carbon stocks in biomass, applying the most accurate biomass equations from the literature was another essential part of this thesis work. It is expected that the biomass equations presented in this thesis will be useful in future research and monitoring. Although most of the forest plantations in Mozambique consist of *Pinus* and *Eucalyptus* (Coetzee and Alves, 2005, MINAG, 2009), biomass equations for these genera are scarce. Prior to this thesis work, site-specific biomass equations for eucalypts were available for *E. grandis* and *E. cloeziana* (Zunguze, 2012). However, the new supplementary data from sampled trees presented in this thesis (**Paper II**) validated the accuracy of the existing equations. On the other hand, there is still a need to develop site-specific biomass equations for *Pinus* species in Mozambique.

Biomass equations are also needed for various natural forest types in Mozambique. Biomass equations have recently been developed for mangrove (Sitoe et al., 2014) and mecrusse woodlands (Magalhães, 2015) in Mozambique, but these equations are not suitable for miombo forests. There are also species-specific biomass equations intended for four different tree species growing in lowland miombo forest (Mate et al., 2014), but they are not suitable for predicting biomass of mixed-species miombo forest. Ryan et al. (2011) developed a mixed-species equation for miombo based on studies near our study area, the Nhambita community in Sofala province, but the sampling was performed in a small geographical area (~0.3 km^2) that did not include regional variation.

In this thesis, a set of interchangeable biomass equations for estimating total aboveground tree biomass of multi-species lowland miombo forest in the Beira development corridor was developed, based on stem diameter at breast height (DBH) and stump diameter (SDI) (Figure 11). The SDI-based equation is principally intended for carbon estimations on harvested trees, and thus to reconstruct the former carbon stocks in forests subjected to logging (Figure 14). The DBH-based equation is recommended for estimating carbon stocks of live trees, due its better precision compared with the SDI-based model.

Both biomass equations include the regional variation (approximately 29,000 km^2) in miombo forest in lowland areas, where the study described in **Paper V** was conducted, and can be applied for estimating total carbon stocks with a high degree of reliability. However, an allometric biomass equation specific for the mountain miombo type in the study area remains to be developed.

Figure 14. Clear-cutting for agriculture in lowland miombo forest in the Beira corridor study area, Mozambique (Photo: Almeida Sitoe).

8 Conclusions

The rapid degradation of miombo forest in Mozambique in recent decades has caused major depletion in carbon stocks, as well as losses of goods and ecosystem services for local communities.

The studies reported in this thesis showed that:

- Total carbon stocks in soil, litter layer and biomass, and net ecosystem production are all significantly higher in *Pinus taeda* and *Eucalyptus grandis* plantations than in adjacent mountain miombo forest.
- Net primary production is higher in *P. taeda* and *E. cloeziana* plantations than in adjacent miombo forest.
- Total soil nitrogen stocks in topsoil layers are significantly higher in non-native plantation stands than in native miombo forest.
- Leaf litterfall, and probably also root litter production, are higher in plantation stands and contribute to the higher soil organic carbon stocks observed in those soils.

Allometric biomass equations are essential tools for estimating carbon stocks in biomass. In this thesis, two biomass functions were developed for estimating aboveground tree biomass of mixed-species lowland miombo forest:

- An equation that estimates biomass based on stem diameter at breast height (1.3 m), which is recommended for estimating carbon stocks of live trees.
- An equation that estimates biomass based on stem diameter at stump height, which is recommended for estimating former carbon stocks in forests subjected to logging.

Overall, the results and analyses presented in this thesis showed that converting degraded mountain miombo in Mozambique to plantations of *P. taeda*, *E. grandis* and *E. cloeziana* is a useful management opportunity if increased carbon stocks and carbon sequestration in biomass and soils is an important aim, provided that the plantations are protected from anthropogenic disturbances, particularly fire. However, it is important to stress that this aim needs to be balanced with other environmental aims, like protection of soils, waters and biodiversity, and must also meet the socio-economic needs of local communities.

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