Review Article

Mixed cropping versus monocultures in plantation forestry: development, benefits, ecosystem services and perspectives for the future

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ABSTRACT

Plantation forests are increasing rapidly in the world in order to alleviate deforestation and degradation of natural forests, along with providing various goods and services. While monoculture plantations have been dominated in practice and well-recorded in research, in face of intensifying climate change and resource scarcity, there is a growing interest in mixed-species plantations. Agroforestry systems are also catching the attention of foresters, smallholders and landowners. However, there are limited studies on successful species mixtures. This paper first reviews the progressions of monocultures and mixed cropping, followed by the comparisons of advantages, disadvantages and effects to the surrounding natural ecosystems between these two types of plantations. The paper further investigates combinations of species with novel traits for efficient use of limiting resources associated with improvement in growth development and production of tree species, as well as examining some other challenges in mixed cropping. Higher species diversity can be achieved in plantations with multiple species. In addition, it is

essential to select and combine tree/crop species in mixtures based on complementary traits that maximise positive and minimise negative interactions and using the advance molecular technologies for genetic analysis. With careful design and proper management, mixed plantations with two, three or four species can be more productive and have more advantages in biodiversity, economy and forest health over monocultures. Many researchers are still working on different projects to explore the potential benefits and to promote the applications of mixed-species plantations and agroforestry.

Keywords: Ecosystem services; Monoculture; Mixed cropping; Species diversity; Complementary trait; Agroforestry

1. Introduction

Plantation forests are expanding readily all over the world. Monocultures have been dominated in practice and well-documented in forest research, but in face of increasing climate change and resource scarcity, there is a growing interest in mixed-species plantation systems. Higher diversity of tree species increases the number of ecological niches, which can further increase the number of associated species, for example, plants in understory and animals by providing them with a better habitat (Larjavaara, 2008). However, there are limited examples of successful mixed-species plantations, especially mixtures with indigenous tropical tree species. The mechanisms of mixing effects in mixed plantations and ideal species combination with complementary traits are largely unknown. In addition, another land use management system, agroforestry, which also involves elements of mixed cropping, is catching the attention of foresters, smallholders and landowners. It is essential to study and understand these kinds of mixed-species systems and their potential socio-economic and ecosystem benefits that could be obtained.

In this review paper, the importance of species diversity to ecosystems and the positive and negative aspects of mixed cropping will be discussed first, followed by discussion on the general plantation forestry trends. The history and current development of monocultures and mixed cropping in forest plantations will be reviewed, respectively. In addition, the advantages and disadvantages of mono-species and mixed-species plantations, along with the effects to the surrounding natural ecosystems will be studied and compared with the support of several species examples. The paper will also examine whether mixed plantations can obtain higher productivity than monocultures, as well as other challenges in mixed cropping. The paper will further focus on the reasons of fewer studies on species mixtures with native tropical tree species and mixtures with non-nitrogen fixing trees. Moreover, identification of complementary traits is difficult. Therefore, in this review, combinations of species with novel traits will be investigated for efficient use of limiting resources, in association with improvement in growth development and production of tree species. It will also discuss different design and management operations that are suitable for adopting species mixtures. Various ongoing projects and programs related to mixed cropping will be explored for the future of forestry and agriculture.

2. Importance of biodiversity

Biodiversity refers to the variety of organisms, including microorganisms, plants, and animals in different ecosystems, such as deserts, forests, coral reefs, etc. (Altieri, 1999; Hamilton, 2005; Carnus et al., 2006; Gugerli et al., 2008). It could be partitioned as species diversity, population diversity, genetic diversity, ecosystem or ecological diversity and molecular diversity (Swift et al., 2004; Srivastava and Vellend, 2005; Mace et al., 2012). The most commonly used representation of ecological diversity is species diversity, which is defined as the number of species and abundance of each species living within a certain location (Hamilton, 2005).

Many species are interconnected and dependent on one another for survival. They perform important ecosystem functions and offer different ecosystem services to support life on Earth and human economies, for instance, water quantity and quality, seed and pollen dispersal, soil formation, nutrient cycles, regulation of pests and human diseases, carbon storage and climate regulation, waste management and cultural services (Balvanera et al., 2006, 2013; Carnus et al., 2006; Mace et al., 2012; Mergeay and Santamaria, 2012). Ecosystems with higher species diversity can be more efficient and are generally more stable and resistant to disaster than those with fewer species, as a substantial number of species consist of many different traits, which can contribute to various functions (Lohbeck et al., 2016). Tropical rainforest is an ecosystem with the greatest biodiversity on Earth. Lefcheck et al. (2015) demonstrated that species-rich communities support higher levels of ecosystem functions. They also showed data that herbivore biodiversity had stronger effects than plant biodiversity, and these effects were consistent in aquatic and terrestrial habitats. Communities with higher diversity of animals also accumulate more biomass (Schneider et al., 2016). It is fundamental to have keystone species, which is either a plant or animal that helps maintain species diversity and the health of ecosystems (Balun, 2017). Without keystone species, the ecosystems would be dramatically altered and species would be adversely affected.

Nowadays, biodiversity is threatened by climate change, pollution, overexploitation of natural resources and habitat loss (Pereira et al., 2012). Loss of biodiversity weakens species connections and impairs the ecosystems, leading to extinction of species and local populations, which will disrupt ecological services. For instance, insects, birds, bats and other animals are known as pollinators. Declines in honey bee (*Apis mellifera*) populations may result in a loss of pollination services with negative impacts on ecology and economy for fruit crops and flowers, which will eventually affect the maintenance of wild plant diversity, wider ecosystem stability, agricultural production, human welfare and global food security (Potts et al., 2010). Not only terrestrial but also regional marine ecosystems, including estuaries, coral reefs, coastal and oceanic fish communities are rapidly losing populations, species or the complete functional groups. Reducing marine diversity will lessen resource availability and rapidly decrease in coastal water quality, ecosystem stability and recovery potential (Worm et al., 2006).

Many studies have shown that plant diversity increases productivity and stability (Tilman et al., 1996, 2006; Weigelt et al., 2009; Jing et al., 2017). Diverse habitats with various plant species can provide forage supporting a wide range of insects and vertebrates (Yadav and Mishra, 2013). Weigelt et al. (2009) and Jing et al. (2017) proved the importance of increasing diversity of plants and other organisms by selecting suitable species with compatible management to achieve both high yields and high persistence in managed grasslands, as well as in other ecosystems. In forestry, species diversity plays a significant role in tree breeding, environmental adaptation and improvement of meeting demands for goods and services.

3. Plantation forestry trends

Due to rapid growth of the world human population and its economies, natural forests in the world are under increasing pressure to meet consumption demands for wood and fibre production, while they are continuously supplying a wide range of social and environmental services (Brown and Ball, 2000). Each year, large areas of natural forests are cleared, degraded, and converted to other land uses (Brown and Ball, 2000; West, 2014). From 2000 to 2010, the global forest area has decreased with a rate of around 13 million hectares per year (FAO, 2006, 2010). As a result, plantation forestry is developed to mitigate future wood shortage problems and produce a huge proportion of world industrial wood and other forest products (Sedjo, 1999; Brown and Ball, 2000; West, 2014).

Plantation forestry refers to cultivated forest ecosystems established through planting or seeding of native or introduced species under the process of afforestation or reforestation (FAO, 2001; Carnus et al., 2006; West, 2014; Nghiem and Tran, 2016). Diverse types of plantations have different purposes, and they are expanding steadily all around the world. Sedjo (2001) reported that it has been common in European regions over the past 200 years; and recently, since the 1960s, intensive forest plantations have also become increasingly ubiquitous in other continents, including North America, South America, Oceania and parts of Asia. The total area of global forest plantations increased from 167.5 million hectares in 1990 to 277.9 million hectares in 2015, and the percentage increased from 4.1 % to 7.0 % over this period (Brockerhoff et al., 2013; Keenan et al., 2015; Payn et al., 2015). Specifically, plantation forests in temperate zones are the largest with the sharpest increase from 1990 to 2015 (Fig. 1). According to FAO (2010), East Asia, Europe and North America are the top three regions with the greatest area of forest plantations (Fig. 2).

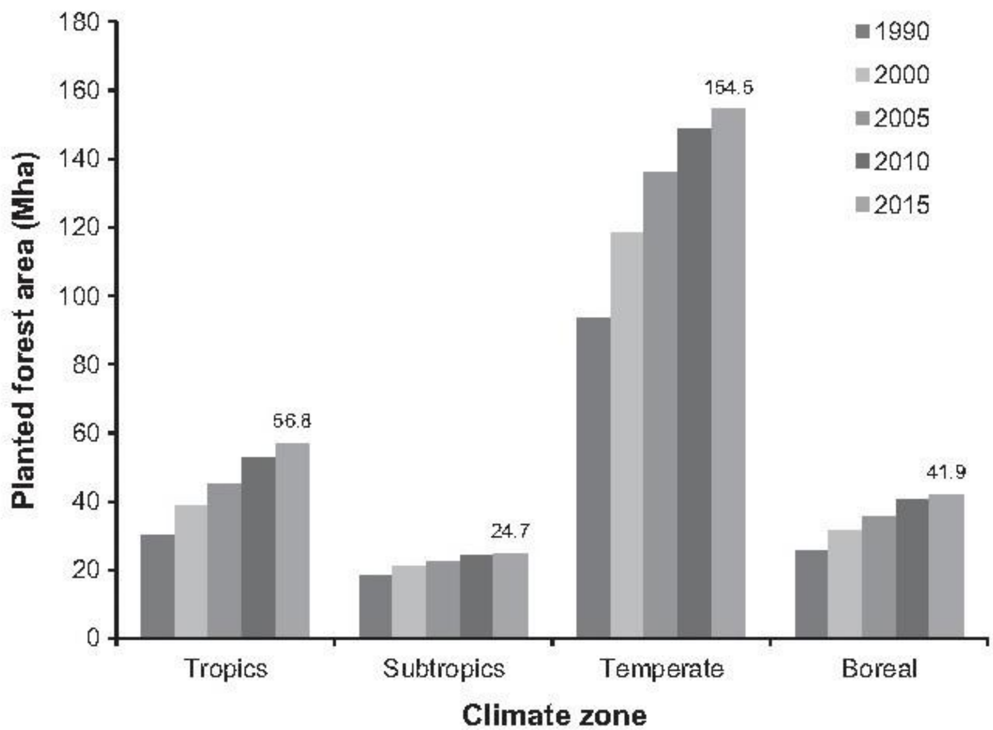

Fig. 1. Trends in area of forest plantations in 1990-2015 in four climate zones. Data source: (Payn et al., 2015, p. 60).

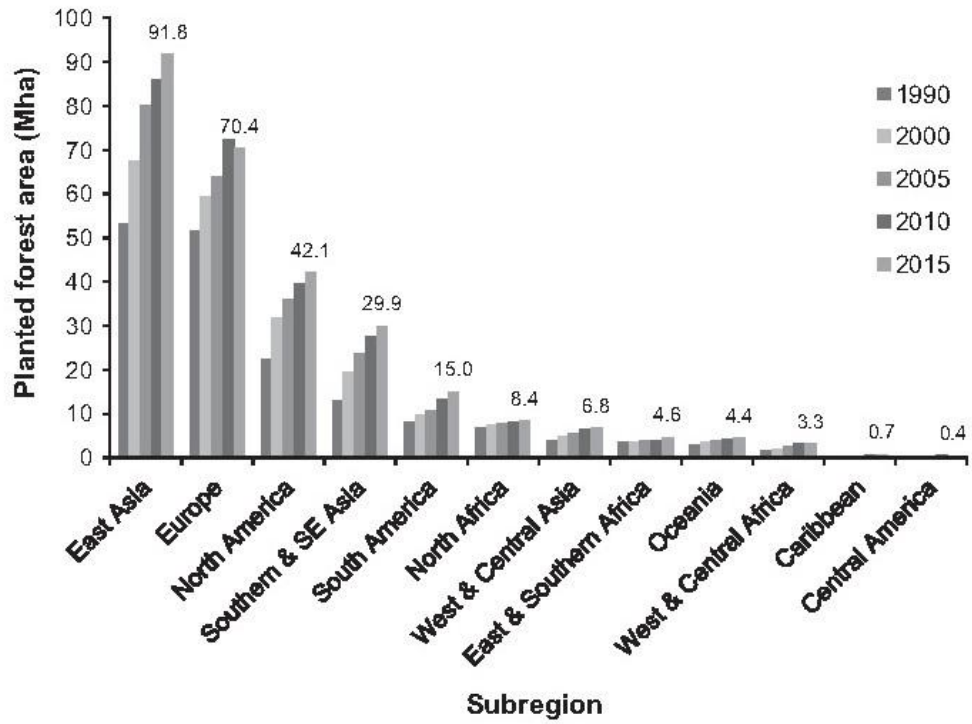

Fig. 2. Planted forest area in 1990-2015 in different regions. Data source: (Payn et al., 2015, p. 60).

Forest plantations have been supplying up to 33 % of the total industrial roundwood in the world, and are projected to meet 50 % of the global industrial roundwood production by 2040 (Kanninen, 2010; Jürgensen et al., 2014). Furthermore, plantation forestry in general is very useful in economy, ecology and society. Planted forests have a vital role in conserving natural forests by relieving deforestation, improving and restoring degraded lands, sequestering carbon dioxide and combating climate change (Sedjo, 1999; Dyck, 2003; Bauhus et al., 2010; Paquette and Messier, 2010; Pawson et al., 2013). Plantations can also be used for regulating the water cycle, reducing soil erosion and alleviating desertification (Bauhus et al., 2010). Economically, planted forests can provide job opportunities and revenue to improve livelihoods of the local communities, as well as strengthening regional and national economies in some countries, such as Brazil, Chile and New Zealand (Nambiar, 1999; Dyck, 2003). Although the effects of plantation forestry on biodiversity are controversial (Braun et al., 2017), numerous studies indicated that forest plantations with proper management can conserve biodiversity by increasing variety of habitats for different plants and animals (Hartley, 2002; Humphrey, 2005; Bremer and Farley, 2010; Irwin et al., 2014; West, 2014; Nghiem and Tran, 2016) and also by lessening the harvesting pressure on native forests (Williams, 2001; Bowyer, 2006). Plantations are important for metapopulations, because they improve connectivity between forest patches and buffer edges across natural forests and non-forest lands (Brockerhoff et al., 2008; Bauhus et al., 2010). Moreover, plantations have contributed to part of the mixed activities on agricultural land, referring to agroforestry—the combination of trees and crops (West, 2014). Both plantations and agroforestry systems can offer different forest products (wood, firewood, mulch), as well as several ecosystem services (Montagnini et al., 2004; Jose, 2009).

4. Monocultures

4.1. Development of monocultures

Many studies have identified that most of the world plantations are monocultures, consisting of a small number of common tree genera, such as *Eucalyptus*, *Pinus*, *Acacia*, *Tectona*, *Picea*, *Pseudotsuga*, *Swietenia* and *Gmelina* (Kelty, 2006; Piotto, 2008; Richards et al., 2010; Alem et al., 2015). Monocultures have been developed for a long time. According to Nichols et al. (2006), the earliest monoculture was documented in 1368, when *Pinus sylvestris* was grown in the Lorenzer Forest near Nuremberg to produce industrial timber. The Western concept of monocultures also developed in the 18th and 19th centuries in Europe because of the scarcity of timber, and the goal was to simplify the structure and speed up the cycles of natural ecosystems, together with producing large amount of wood within the shortest time (Baltodano, 2000; Griess and Knoke, 2011).

4.2. Positive aspects of monocultures

The advantages of monocultures are well understood and documented. They are used for treating wastewater and improving water quality (Minhas et al., 2015), rehabilitating deforested watersheds and degraded landscapes (Parrotta, 1999). Many different timber and other forest products can be grown in this kind of large-scale plantation system as well. Monocultures for wood and fibre products are dominated in the tropics (Kanninen, 2010). Fast-growing, exotic and low-density wood species, such as *Eucalyptus*, *Pinus* and *Acacia* are largely used for timber, paper pulp, charcoal and fuel, because they have short rotation period and have advantages in competing for light, nutrients and water resources over native plants (Li et al., 2014; Nguyen et al., 2014; Chaudhary et al., 2016). In temperate and boreal zones, *Populus* is planted to provide shelter, protect soil and water resources, and sometimes produce wood fuel. *Salix* species can be also used as potential bioenergy crops (Brown, 2000). According to Chaudhary et al. (2016), non-timber monoculture plantations, particularly in tropical regions, can supply palm oil, rubber, plantain or bamboo. Countries in South America, Asia and southern Africa are promoting monocultures of pine and eucalyptus for paper pulp supply (Table 1). There is also a fast expansion of rubber and oil palm monocultures in South-East Asia to meet the increasing world demand.

Table 1

Fast-growing plantations by species, countries and mean annual increment. Data source: (Kanninen, 2010, p. 10).

Species	Mean annual increment (m^3/ha/year)	Rotation length (years)	Estimated extent as fast-growing plantation only (1000 ha)	Main countries (in decreasing order of importance)
Eucalyptus grandis and various eucalypt hybrids	15-40	5-15	± 3700	Brazil, South Africa, Uruguay, India, Congo, Zimbabwe
Other tropical eucalypts	10-20	5-10	± 1550	China, India, Thailand, Vietnam, Madagascar, Myanmar
Temperate eucalypts	5-18	10-15	± 1900	Chile, Portugal, NW Spain, Argentina, Uruguay, South Africa, Australia
Tropical acacias	15-30	7-10	± 1400	Indonesia, China, Malaysia, Vietnam, India, Philippines, Thailand
Caribbean pines	8-20	10-18	± 300	Venezuela
Pinus patula and *P. elliottii*	15-25	15-18	± 100	Swaziland
Gmelina arborea	12-35	12-20	± 100	Costa Rica, Malaysia, Solomon Islands
Paraserianthes falcataria	15-35	12-20	± 200	Indonesia, Malaysia, Philippines
Poplars	11-30	7-15	± 900	China, India, USA, Central and Western Europe, Turkey

Fig. 3. Monoculture plantation of eucalyptus for paper manufacturing at Aracruz Celulose in Barra do Riacho, Brazil. Data source: (https://www.theguardian.com/environment/2011/sep/26/monoculture-forests-africa-south-america; Photo Credit: Paulo Fridman).

Fig. 4. Monoculture plantation of longleaf pine in the U.S. Data source: (Shelton, 2012; https://www.fws.gov/endangered/map/ESA_success_stories/GA/GA_story1/index.html; Photo Credit: Randy Browning, USFWS).

Fig. 5. Industrial-scale rubber tree monoculture plantation in Cambodia. Data source: (https://ewarrenthomas.com/research; Photo Credit: Eleanor Warren-Thomas).

In monocultures, all the site resources are mainly focused on the growth of single species with the most desirable characteristics, such as growth rate and wood quality (Kelty, 2006; Piotto, 2008; Moghaddam, 2014). Tree species in monocultures are mostly even-aged and planted at a high density in accessible areas, which allow the plantations to have easy management and high resilience; thus, higher yields per hectare and more efficient harvest resulting in uniform products can be obtained (Baltodano, 2000; Kelty, 2006; Nichols at al., 2006; Piotto, 2008).

4.3. Negative aspects of monocultures

Research by various authors have criticised single-species monocultural plantations as supposedly having several negative social and environmental impacts in spite of the recognised economic benefits (Erskine et al., 2006; Alem et al., 2015). Regarding the social impacts, the introduction of large-scale plantations often leads to the change in the ownership from local communities to large private companies, hence, resulting into a loss of traditional goods and cultures, customary rights, and livelihoods associated with forced resettlement and unequal distribution of resources (Baltodano, 2000; Colchester, 2006). Moreover, effects on the environment include the loss of soil productivity and fertility, disruption of hydrological cycles, risks associated with plantation forestry practices (e.g., introduction of exotic species), risks of promoting pests and diseases, higher risks of adverse effects of storms and fire, and negative impacts on biodiversity (Baltodano, 2000; Evans, 2001; Bowyer, 2006).

Monoculture plantations may deplete soil, causing soil erosion and degradation (Baltodano, 2000; Bowyer, 2006). Tree harvesting by machines can promote soil compaction, which will adversely affect the growth of understory. Single-species plantations are also not efficient in trapping nutrients, because fewer roots exist near the surface, which may further lead to significant loss of nutrients from the harvest sites. In addition, some species, such as *Eucalyptus* and *Gmelina* can acidify soil, and in addition *Gmelina* can release specific substances that inhibit the growth of other plant species (Baltodano, 2000). There are some concerns about depletion of soil moisture and reduced stream flow in plantations. Some researchers have observed that particular species (e.g., *Eucalyptus*) consumes more water than the others in natural forests, which may draw down the water table in some regions (Baltodano, 2000; Morris et al., 2004; Bowyer, 2006). Furthermore, monocultures are more susceptible to pests and diseases. Owing to the uniform genetic composition and closeness of tree species in monocultures, they can provide a huge food source and ideal habitat for insects and pathogens, which will consequently give rise to rapid colonisation and spread of infection (Hartley, 2002; Bowyer, 2006; Carnus et al., 2006; Brockerhoff et al., 2013; Moghaddam, 2014).

The link between plantation forestry and biodiversity is still debatable as mentioned before, because many researchers suggested that plantation monocultures have a potential to provide habitats for indigenous flora and fauna and enhance biodiversity in degraded lands (Cuong et al., 2013). However, an increasing number of studies have discovered that monoculture plantations have lower levels of biodiversity than surrounding native forests, and some of them have considered exotic monocultures as “biological deserts” (Bowyer, 2006; Bremer and Farley, 2010; Brockerhoff et al., 2013; Pawson et al., 2013). Harvesting monoculture stands by clearcutting is one of the possible reasons explaining the dramatic alteration of habitat. Furthermore, uniform rows of monoculture plantations are completely opposite to diversity, and they have been found to be poor habitat for native birds (Subasinghe et al., 2014; Chaudhary et al., 2016; Dislich et al., 2017). Nevertheless, Kanowski et al. (2005) noted that the effects of plantations on biodiversity vary from case to case in terms of design, including tree species, stand density, the retention or restoration of native forests, as well as management, such as harvest regimes and chemical applications, together with factors related to landscape context.

Felton et al. (2010) reviewed negative ecological and environmental impacts of monoculture plantations of spruce and showed that these plantations have lower resistance to biotic and abiotic disturbances aggravated by changing climates. Moreover, expanding spruce monocultures in southern Sweden has resulted in population declines and increased risks of extinction for numerous forest dependent taxa. The soils in those plantations become more acidic as well, and subsequently generate unfavorable outcomes for biodiversity and other land uses in the long term. However, potential risks can be minimised with proper planning and good management practices of monocultures (Bowyer, 2006; Kelty, 2006).

5. Mixed cropping

5.1. Advancement of mixed cropping

Plantations which are diverse in genotypes, species, structures and functions, are acclaimed as more environmental friendly and sustainable plantation systems over monocultures, especially in case of mixing indigenous species (Manson et al., 2013). However, we are unaware of a single specific definition for mixed cropping or, in other words, mixed-species plantation (Griess and Knoke, 2011; Felton et al., 2016). Mixtures can be arranged in many ways with variations in species composition and dominance, spatial arrangement and age structure (Ashton and Ducey, 1997). Current studies on multi-species plantations are limited, and mixtures of native trees are relatively uncommon. It makes more interesting and important establishing and exploring this type of diversified plantation system (Ashton and Ducey, 1997; Forrester et al., 2005; Nichols et al., 2006). There is also wealth of research on the growth interactions with non-nitrogen fixing species in mixed plantations and their effects on the regeneration of woody plants (Alem et al., 2015). It was shown that potential benefits can be obtained from carefully designed mixed-species plantations (Piotto, 2008; Griess and Knoke, 2011; Manson et al., 2013; Nguyen et al., 2014).

There are several cases of mixed-species plantations that have been successful and popular over the centuries. According to Kelty (2006) and Nichols et al. (2006), mixing larch trees with pine in Europe had already been recorded in 1910s, and mixtures with other species, such as alder, oak and beech, were continued to develop for early income stream. Since the 1980s, rigorous experimental research focusing on the comparison of mixtures and monocultures were set up with comprehensive data collection (Piotto, 2008; Plath et al., 2011). The applications of suitable tree species in mixed plantations have been mainly demonstrated in Europe and North America, but a few studies have been also documented in the tropics with some notable examples of mixing *Eucalyptus*, *Albizia* and *Acacia* (Ashton and Ducey, 1997). Furthermore, there has been a gradual decrease in area of single-species plantations, and this resulted in a steady progression of species mixtures with the objectives of increasing productivity, resistance and resilience or converting plantations from conifers to broadleaved species (Bravo-Oviedo et al., 2014). Generally, mixed-species plantations consist of two, three or even four species of plants, but it is possible to have more diverse and complex mixtures (Nguyen et al., 2014).

Agroforestry also represents an important type of mixed cropping system, where woody perennials (trees and shrubs) are grown in association with agricultural crops and pastures on the same land and at the same time (Malézieux et al., 2009). Agroforestry systems have been practiced in both tropics and temperate zones for thousands of years until the Middle Ages. Then, they started to decline while crop rotation was evolved for soil protection (Smith, 2010b). In the late 1970s, a new concept of agroforestry was introduced again and encouraged by many European policies in the 1990s, aiming for diverse productions coupled with conservation of resource and environment (Smith, 2010b; Nerlich, 2013). Silvoarable and silvopasture are the current major agroforestry practices in Europe based on using a range of dominant tree species (Mosquera-Losada et al., 2009).

5.2. Advantages of mixed cropping

There are abundant evidences that planting multiple species can gain numerous economic, environmental and social benefits (Hartley, 2002; Forrester et al., 2005; Plath et al., 2011; Pawson et al., 2013; Carnol et al., 2014; Alem et al., 2015; Drössler et al., 2015; Nguyen et al., 2015). First of all, species mixtures can maximise the use of resources, and consequently increase stand-level productivity and carbon sequestration. Several studies have found that mixed plantations are more productive in comparison with monocultures (Kanowski et al., 2005; Petit and Montagnini, 2006; Richards et al., 2010; Zhang et al., 2012; Pretzsch and Schütze, 2016). An example from Chomel et al. (2014) demonstrated that mixing hybrid poplar and white spruce increased wood production of poplar and sequestrated more carbon than monocultures of either poplar or white spruce. Mixtures with stratification can also enhance individual-tree growth rates and stem quality of species in upper canopies, whilst minimising the proportion of taller species that can reach the highest production (Kelty, 2006; Piotto, 2008). However, uncertainty remains about mixtures achieving greater productivity than monocultures (Carnus et al., 2006; Erskine et al., 2006; Piotto, 2008; Griess and Knoke, 2011; Drössler et al., 2015).

In addition, Forrester et al. (2006) reported that several examples of mixing eucalyptus and nitrogen-fixing species increased productivity and nutrient cycling rates, and they had better results than monocultures. The study from Forrester et al. (2010) also suggested that mixtures of *Eucalyptus* and *Acacia* can enhance water-use efficiency, but there are still cases of reduced productivity in mixtures (Binkley et al., 2003; Kelty, 2006). Another advantage of mixed cropping over monocultures is the promotion of diversifying production under different rotation periods (Forrester et al., 2006). Mixed plantations are more resistant to damage caused by storms, insects or diseases (Hartley, 2002; Nichols et al., 2006; Griess and Knoke, 2011). Some species can act as nurse to other tree species, and mixtures of fast-growing and slower-growing species can produce timber and more valuable wood products while reducing risks of soil erosion and providing shelter and protection against frost or pests (Montagnini et al., 2004; Petit and Montagnini; 2006). Taller species in mixtures can also provide shading to shorter species, resulting in less branching of the smaller ones, which may eventually improve the wood quality (West, 2014). Moreover, mixed plantations could be more efficient in filtering of atmospheric pollutants (e.g., sulphur and chlorine) in the areas with heavy precipitation (Zhao et al., 2017). There is a potential of using more complex mixtures with five to seventy species for restoration of degraded lands (Kelty, 2006; Nguyen et al., 2014). For ecological benefits, Felton et al. (2016) proved that spruce-birch and spruce-pine polycultures did not only simply support aesthetic and recreational values, but they also increased avian diversity with special composition of bird species.

Correspondingly, agroforestry systems have been well recognised as an improvement on monocultures and being closer to native forests (Chaudhary et al., 2016). They can provide a wide variety of goods (e.g., rubber, coconut, coffee or cacao), reduce poverty, increase carbon storage, enhance soil fertility and improve water and air quality (Alavalapati et al., 2004; Jose, 2009). Growing trees with agricultural crops can also produce high-value wood products and bioenergy, minimise the risk of pest outbreaks and enhance biodiversity (Nerlich et al., 2013). There are several successful agroforestry examples. For instance, Pelleri et al. (2013) presented a mixed plantation of walnut, poplar and some other nurse trees (e.g., black alder and hazel), which had favourable impacts on the growth of both walnut and poplar, farm economics, and landscape quality, as well as this plantation was less prone to disturbances. Mutanal et al. (2007) showed that mixed cropping of fast-growing tree species and tamarind had higher yields and better growth performance in comparison with monocultures, as well as having the capability to prevent soil erosion and increase biodiversity.

Fig. 6. Mixed-species stand of white spruce (*Picea glauca*) under aspen (*Populus tremoluides*) in Canada. It is a very common natural mixture in boreal Canada. Its management and productivity have been studied in detail. Here the aspen is a pioneer regenerated after large disturbances such as fire, and the white spruce are naturally regenerated afterwards. Data source: (Fjellstad, 2016; https://www.nordgen.org/en/establishment-high-productive-mixtures/; Photo Credit: Phil Comeau).

Fig. 7. A small mixed species plantation of trees in the midst of grazing land near Forden, Powys, Great Britain. Data source: (http://www.geograph.org.uk/photo/643952; Photo Credit: John Haynes).

Fig. 8. An alley cropping agroforestry system growing hybrid poplar and wheat in France. Data source: (http://www.4bm.ca/services/agroforestry.cfm; Photo Credit: Vincent Chifflot).

Table 2

Levels of risks for several forest types due to different factors. Data source: (Dedrick et al., 2007, p. 80).

Factor	Eucalyptus	Poplar	Short rotation pine	Long rotation pine	Spruce monocultures	Mixed forests
Climatic	2-3	2-3	2	2-3	3	1-2
Static stability	2	2	1-2	1	3	1-2
Anthropogenic	1	2	1	1-2	3	1
Insects	3	2-3	2-3	2	3	2
Diseases	3	3	3	2	3	2
Wild game	1	1	1	3	3	3
Fires	2	1	3	3	1	1-3
Total	14-15	13-15	13-15	14-16	19	11-14

Table 2 demonstrates an evaluation of risks for six different forest management approaches with scores 1–3 (low to high). The evaluated risk factors included climate impacts, stability, human impacts, insects, diseases, wild game and fires. Mixed forests had the lowest scores in total among all the management strategies, and contrastingly, spruce monocultures had the highest. This implies that mixed plantations are certainly less susceptible to biotic and abiotic disturbances, and it is a good evidence showing that species mixtures are preferable to monocultures.

5.3. Disadvantages of mixed cropping

There are some disadvantages in species mixtures. Mixtures in tropical regions may negatively affect biodiversity. For example, mixed-species plantations have lower diversity than local rainforests in Australia, and they support fewer rainforest bird species than monocultures (Kanowski et al., 2005). Species mixtures in some conditions will also reduce soil fertility and productivity because of asymmetric competition (Forrester et al., 2005; Petit and Montagnini, 2006; Manson et al., 2013). Furthermore, improper choice of tree species or crops for mixtures can create local conditions that increase the risk of disease outbreaks (Gebru, 2015; Thomsen, 2016). For agroforestry systems, they have very few drawbacks, but setting up a successful one is very challenging and time-consuming.

5.4. Combination of species with complementary traits

A great number of studies have indicated that it is important to select species in mixtures with complementary structural and functional traits, such as shade tolerance, height growth rate, crown structure, foliar and root phenology and root depth (DeBell and Harrington, 1993; Kelty, 2006; Nichols et al., 2006; Nguyen et al., 2015; Schuler et al., 2017). Therefore, a successful mixed-species plantation may combine fast-growing with slow-growing species, short-lived with long-lived species, light demanding with shade tolerant species, shallow with deep rooting species, nitrogen-fixing with non-nitrogen-fixing species or slim-crowned and height oriented with wide-crowned and more laterally expanding species (Forrester et al., 2005, 2006; Yadav and Mishra, 2013; Pretzsch, 2014; Nguyen et al., 2015). In such cases, species can potentially increase light interception, biomass production, biodiversity and resistance to disturbances (Kelty, 2006; Pretzsch, 2014). There is also a useful online platform named TRY, which offers a database of global plant traits for researchers (Kattge et al., 2011).

Modern molecular technologies including marker-assisted selection (MAS) based on quantitative trait loci (QTLs), genomic selection (GS) based on genome-wide single nucleotide polymorphism (SNPs) associations with important traits, and genetic modification are widely used in tree breeding (Moose and Mumm, 2008). MAS can greatly increase the efficiency and effectiveness in plant breeding compared with traditional breeding methods. At first, it requires the determination of DNA markers that are tightly linked to important genes or QTLs of interest, and afterwards, breeders may use the specific DNA marker alleles as a powerful diagnostic tool to identify plants which carry the necessary genes or QTLs (Collard et al., 2005). This method has proven to be successful in breeding of various crop species (e.g., maize, rice, barley and soybean), and it has the advantages of improving yields along with increasing abiotic and biotic stress resistance (Francia et al., 2005).

However, polygenic inheritance of traits is a major limitation of MAS. GS can overcome the limitation of MAS by using whole genome molecular markers and high throughput genotyping (either by using high-density SNP genotyping assays, such as Illumina Infinium system, or genotyping by sequencing with next generation sequencing (NGS) platforms) to improve quantitative traits with higher accuracy in large plant breeding populations (Desta and Ortiz, 2014; Lin et al., 2014; Iwata et al., 2016; Grattapaglia, 2017; Jonas et al., 2018). Genetic values of selection candidates can be predicted based on the genomic estimated breeding values (GEBVs) through this approach (Newell and Jannink, 2014). Additionally, agro-morphological traits can be introgressed to well-adapted crop species by the integration of selected candidates with the highest GEBVs and other breeding programs (Fig. 9).

In addition, the use of genetic modification provides a unique opportunity to improve novel traits of plants and accelerate tree breeding, resulting in an increase and reliable wood production in future (West, 2014; Häggman et al., 2016). Examples of agronomic traits, including enhanced herbicide resistance, enhanced resistance to pests, diseases and abiotic stresses, modified lignin content and improved wood quality, could be attained by altering the expression of specific gene(s) and incorporating new genes into the plant genomes (Harfouche et al., 2011) or by genome editing (Songstad et al., 2017). Nevertheless, these techniques are still relatively new in forestry, and there are some risks or issues related to environmental, economic and social aspects. Therefore, more laboratory genetic engineering studies and tests are required for approving genetically modified trees and crops.

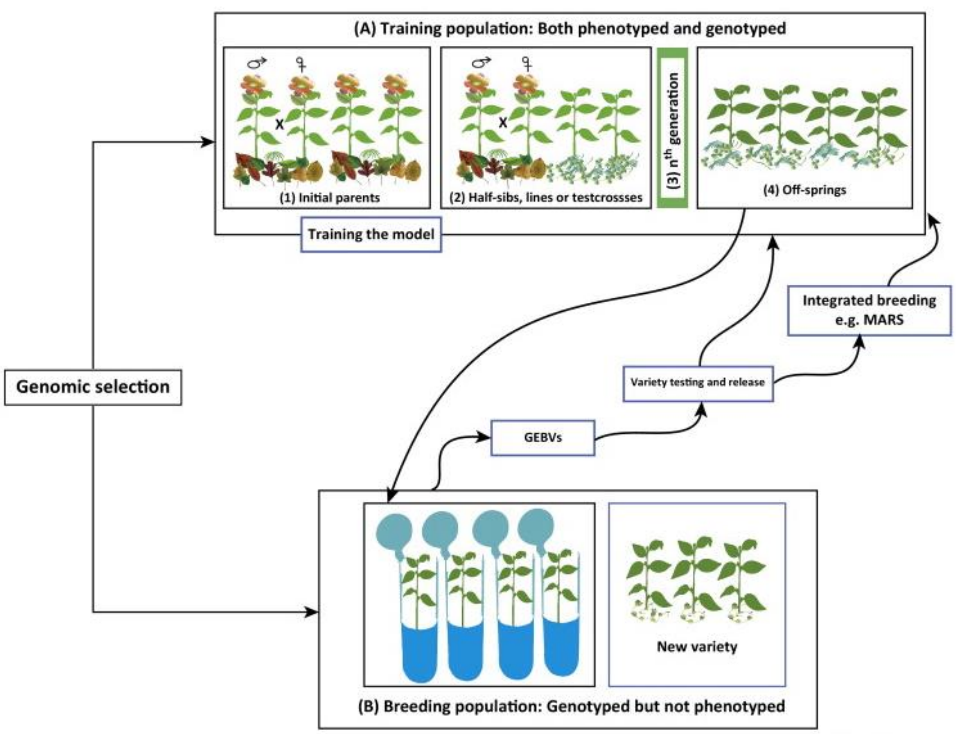

Fig. 9. Application of genomic selection in crop and tree breeding. Data source: (Desta and Ortiz, 2014, p. 594).

Recently, several projects have been aimed at the identification of genetic control of the complementary plant traits in the mixed woody species plantations. For example, the IMPAC^3 project identifies novel traits in mixed cropping of poplar (*Populus* sp.) and black locust (*Robinia pseudoacacia*). Activity and gene expression are currently studied in different environmental conditions with the use of transcriptome analysis based on the NGS (IMPAC^3, 2014; Kuchma et al., 2017). Mixed plantations of poplar and black locust used in this project is a typical example of mixing nitrogen-fixing with non-nitrogen-fixing species assuming that poplar may gain nitrogen from black locust, and that regional ecosystem in association with higher yields can also benefit from mixed cropping (Zhai et al., 2006).

In intercropping system, diverse germplasm can be used in trials for assessing genotypes with favourable yield or quality, and it is also considerable to breed plants with traits that are beneficial to a companion crop (Brooker et al., 2015). Furthermore, plant breeding research and cultivar development are crucial for improvement of food production, thus, the availability of diverse genetic sources can enhance food security together with agricultural sustainability (Govindaraj et al., 2015).

5.5. Challenges of mixed cropping

However, several obstacles exist in the expansion of polyculture plantations. Firstly, species mixtures require complicated forest management operations, and some foresters have the perception that mixed-species plantings reduce productivity (Pawson et al., 2013; Felton et al., 2016). Secondly, there are limited evidence and knowledge for matching species to site conditions, as well as growth strategies of native species in mixed plantations (Nichols et al., 2006; Manson et al., 2013; Nguyen et al., 2014). It is uncommon to have mixtures with more than four species because of the difficulty in matching suitable characteristics. In newly developed mixtures, there is a chance that tree species suffer from both interspecific and intraspecific competition (Nguyen et al., 2014). There are also very few instructions for designing and managing mixed-species systems (Fischer and Vasseur, 2002; Nguyen et al., 2005). Furthermore, the shortage of time, awareness and training between farmers and landowners are the additional restrictions of applying agroforestry systems (Smith, 2010a; Wilson and Lovell, 2016).

6. Future perspectives of mixed cropping

To gain a better understanding and sustainable use of mixed cropping, many researchers keep exploring the potential benefits for the future of forestry and agriculture. In forestry, KROOF project will use tree and stand-level growth reactions induced by a drought experiment to examine whether spruce suffers more in mixtures (e.g., spruce with beech) than in monocultures under limited water supply (Pretzsch et al., 2014). Additionally, the purposes of developing the CommuniTree Carbon program are to improve livelihoods of small-scale farmer families, sequestrate carbon, and enhance biodiversity and environment by planting mixtures with five native tree species in Nicaragua (Baker et al., 2014). In agriculture, Iijima et al. (2016) suggested a new concept of mixing wet and dryland crops (e.g., pearl millet and sorghum with rice), which will strengthen the flood tolerance of upland crops. Another research from Thünen-Institut is studying the potential of mixing maize with runner beans and expecting an increase in production together with improvement of protein and energy supply in monogastrics and ruminants (Hamburdă et al., 2015). The agroforestry systems can produce more bioenergy and replace the use of fossil fuels in future (Nerlich et al., 2013). Furthermore, a project named SidaTim will assess and model the economic and ecological potentials of growing *Sida hermaphrodita* along with valuable timber trees (e.g., walnut and cherry) to promote a diversified agricultural system in different European countries (FACCE SURPLUS, 2016). This type of agroforestry will provide extra income for farmers, reduce erosion, act as windbreaks and improve ecological and aesthetic values.

There are two more large-scale agroforestry projects taking place—AGFORWARD and BREEDCAFS. The former one will give an in-depth analysis about the agroforestry systems in Europe, develop and assess innovative agroforestry designs and practices with favourable impacts, and encourage a wider adoption of suitable agroforestry in Europe through dissemination and policy (AGFORWARD, 2014). The BREEDCAFS project is led by CIRAD and developed to address climate change through coffee breeding (CIRAD, 2017). This project may help increase smallholder farmers' earnings, produce coffee varieties with high quality for coffee industry, as well as obtaining understanding of coffee physiology through the combination of phenotyping and advanced DNA analysis (WORLD COFFEE RESEARCH, 2017).

Future research should be done on nutrition in mixed-species plantations, especially with non-nitrogen fixing mixtures due to less attention to other nutrients (Nichols et al., 2006). Besides, a special type of mixed-species planting (i.e. rainforestation farming), which was first developed in the Philippines, should be widely promoted in tropical regions (Nguyen et al., 2014). It is a novel strategy that combines the concepts of rural development, resource management, biodiversity conservation and landscape restoration by mixing indigenous tree species with local agricultural crops. This system can provide sustainable income to smallholders, create community forestry and save the endangered species, such as the tiniest ape, *Tarsius syrichta* (Göltenboth and Hutter, 2004). Most importantly, there is a necessity for greater amount of evidence, education, funding, incentives, innovative experiments with wider range of tree species and analyses for polyculture expansion (Nichols et al., 2006; Moghaddam, 2014). In agroforestry, it is necessary to raise awareness and demonstrate practical management skills to farmers and landowners, and there is a potential of establishing more agroforestry systems in temperate regions (Smith, 2010a).

7. Conclusion

In summary, there is a global trend of increasing forest plantations to relieve the pressure of deforestation and degradation of natural forests, in addition to meet demands of timber products and forest services. The majority of world plantation forests are monocultures with certain dominant tree species, which are favoured for timber production due to the uniformity of trees and easy management. Monocultures are still expanding in South-East Asia. Meanwhile, mixed-species plantations are growing and becoming more popular, since they have been found to have more benefits in biodiversity, economy, forest health and occasionally in productivity compared with monospecific plantations. Higher species diversity can be achieved in plantations with multiple species (Larjavaara, 2008).

Undoubtedly, there are also challenges in designing, planting and managing species mixtures. Mixed plantations can have negative or positive effects on tree growth (Piotto, 2008). It is necessary to select and combine tree or crop species in mixtures with complementary traits that maximise positive and minimise negative interactions using the advance molecular technologies (Brooker et al., 2015). With careful design and appropriate management, mixed plantations with three or four species can be more productive and have more advantages over disadvantages. As a result, mixed-species plantations and agroforestry should be broadly promoted and adopted as they can produce more economic and ecological gains, and contribute to food security.

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References

AGFORWARD, 2014. *AGroFORestry that Will Advance Rural Development* is a research project funded by the European Union’s Seventh Framework Programme (FP7) for Research and Technological Development (January 2014 - December 2017). Retrieved from http://www.agforward.eu/index.php/en/home-redirect.html (August 12, 2017)

Alavalapati, J., Shrestha, R., Stainback, G., Matta, J., 2004. Agroforestry development: an environmental economic perspective. Agroforestry Systems 61(1-3), 299-310. doi:10.1023/b:agfo.0000029006.64395.72

Alem, S., Pavlis, J., Urban, J., Kucera, J., 2015. Pure and mixed plantations of *Eucalyptus camaldulensis* and *Cupressus lusitanica*: their growth interactions and effect on diversity and density of undergrowth woody plants in relation to light. Open Journal of Forestry 5(4), 375-386. doi:10.4236/ojf.2015.54032

Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment 74(1-3), 19-31. doi:10.1016/s0167-8809(99)00028-6

Ashton, P.M.S., Ducey, M.J., 1997. The development of mixed species plantations as successional analogues to natural forest. In Landis, T.D.; South, D.B., tech. coords. *National Proceedings: Forest and Conservation Nursery Associations*. Portland, OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, pp. 113-126.

Baker, K., Baumann, D., Michaud, J., Van Mossel-Forrester, B., 2014. Technical Specification. Mixed Species Forest Plantation. Registered Plan Vivo Project: The CommuniTree Carbon Program, 1-73 p. https://takingroot.org/wp-content/uploads/2015/04/takingroot-mixed-species-planting.pdf

Baltodano, J., 2000. Monoculture forestry: a critique from an ecological perspective. In Tree Trouble: a compilation of testimonies on the negative impact of large-scale monoculture tree plantations prepared for the 6th COP of the FCCC. Friends of the Earth International, pp. 2–10.

Balun, R., 2017. The Importance of Species Diversity to the Ecosystem. Retrieved from http://sciencing.com/importance-species-diversity-ecosystem-6508788.html (August 17, 2017)

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9(10), 1146-1156. doi:10.1111/j.1461-0248.2006.00963.x

Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A., Byrnes, J., O'Connor, M.I., Hungate, B.A., Griffin, J.N., 2013. Linking biodiversity and ecosystem services: current uncertainties and the necessary next steps. BioScience 64(1), 49-57. doi:10.1093/biosci/bit003

Bauhus, J., Pokorny, B., van der Meer, P.J., Kanowski, P.J., Kanninen, M., 2010. Ecosystem goods and services—the key for sustainable plantations. In J. Bauhus, P. van der Meer, and M. Kanninen (Eds.), Ecosystem Goods and Services from Plantation Forests. London, UK: Earthscan, pp. 205-227.

Binkley, D., Senock, R., Bird, S., Cole, T.G., 2003. Twenty years of stand development in pure and mixed stands of *Eucalyptus saligna* and nitrogen-fixing *Facaltaria moluccana*. Forest Ecology and Management 182(1-3), 93-102. doi:10.1016/S0378-1127(03)00028-8

Bowyer, J. L., 2006. Forest plantations threatening or saving natural forests? Arborvitae (IUCN/WWF Forest Conservation Newsletter) 31, 8-9.

Braun, A.C., Troeger, D., Garcia, R., Aguayo, M., Barra, R., Vogt, J., 2017. Assessing the impact of plantation forestry on plant biodiversity: a comparison of sites in Central Chile and Chilean Patagonia. Global Ecology and Conservation 10, 159-172. doi:10.1016/j.gecco.2017.03.006

Bravo-Oviedo, A., Pretzsch, H., Ammer, C., Andenmatten, E., Barbati, A., Barreiro, S., Brang, P., Bravo, F., Coll, L., Corona, P., den Ouden, J., Ducey, M.J., Forrester, D.I., Giergiczny, M., Jacobsen, J.B., Lesinski, J., Löf, M., Mason, W.L., Matovic, B., Metslaid, M., Morneau, F., Motiejunaite, J., O'Reilly, C., Pach, M., Ponette, Q., den Rio, M., Short, I., Skovsgaard, J.P., Soliño, M., Spathelf, P., Sterba, H., Stojanovic, D., Strelcova, K., Svoboda, M., Verheyen, K., von Lüpke, N., Zlatanov, T., 2014. European mixed forests: definition and research perspectives. Forest Systems 23(3), 518-533. doi:10.5424/fs/2014233-06256

Bremer, L.L., Farley, K.A., 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. Biodiversity and Conservation 19(14), 3893-3915. doi:10.1007/s10531-010-9936-4

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Ferraz, S.F., 2013. Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. Forest Ecology and Management 301, 43-50. doi:10.1016/j.foreco.2012.09.018

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity and Conservation 17(5), 925-951.

Brooker, R.W., Bennett, A.E., Cong, W.F., Daniell, T.J., George, T.S., Hallett, P.D., Hawes, C., Iannetta, P.P.M., Jones, H.G., Karley, A.J., L, Li., McKenzie, B.M., Pakeman, R.J., Paterson, E., Schöb, C., Shen, J., Squire, G., Watson, C.A., Zhang, C., Zhang, F., Zhang, J., White, P.

J., 2015. Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. New Phytologist 206(1), 107-117. doi:10.1111/nph.13132

Brown, C., 2000. The global outlook for future wood supply from forest plantations. Working Paper No: GFPOS/WP/03. Rome, Italy: FAO.

Brown, C., Ball, J., 2000. World view of plantation grown wood. Paper presented at the XXI IUFRO World Conference, Kuala Lumpur, Malaysia. Retrieved from http://www.fao.org/forestry/25860-0bc06e1b1190f66bb48651bfd756f37fd.pdf (July 25, 2017)

Carnol, M., Baeten, L., Branquart, E., Grégoire, J.C., Heughebaert, A., Muys, B., Ponette, Q., Verheyen, K., 2014. Ecosystem services of mixed species forest stands and monocultures: comparing practitioners' and scientists' perceptions with formal scientific knowledge. Forestry: An International Journal of Forest Research 87(5), 639-653. doi:10.1093/forestry/cpu024

Carnus, J.M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Ponette, Q., Walters, B., 2006. Planted forests and biodiversity. Journal of Forestry 104(2), 65-77.

Chaudhary, A., Burivalova, Z., Koh, L. P., Hellweg, S., 2016. Impact of forest management on species richness: global meta-analysis and economic trade-offs. Scientific Reports 6, 23954. doi:10.1038/srep23954

Chomel, M., DesRochers, A., Baldy, V., Larchevêque, M., Gauquelin, T., 2014. Non-additive effects of mixing hybrid poplar and white spruce on aboveground and soil carbon storage in boreal plantations. Forest Ecology and Management 328, 292-299. doi:10.1016/j.foreco.2014.05.048

CIRAD, 2017. BREEDCAFS, an EU research project adapting coffee varieties for agroforestry. Retrieved from http://www.cirad.fr/en/news/all-news-items/articles/2017/science/breedcafs-new-coffee-varieties-for-agroforestry (August 12, 2017)

Colchester, M., 2006. Plantations for people? Arborvitae (IUCN/WWF Forest Conservation Newsletter) 31, 7.

Collard, B.C., Jahufer, M.Z., Brouwer, J.B., Pang, E.C., 2005. An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: the basic concepts. Euphytica 142(1-2), 169-196. doi:10.1007/s10681-005-1681-5

Cuong, C. V., Lamb, D., Hockings, M., 2013. Simple plantations have the potential to enhance biodiversity in degraded areas of Tam Dao National Park, Vietnam. Natural Areas Journal 33(2), 139-147. doi:10.3375/043.033.0203

DeBell, D.S., Harrington, C.A., 1993. Deploying genotypes in short-rotation plantations: mixtures and pure cultures of clones and species. The Forestry Chronicle 69(6), 705-713. doi:10.5558/tfc69705-6

Dedrick, S., Spiecker, H., Orazio, C., Tomé, M., Martinez, I., (Eds.), 2007. Plantation or conversion—the debate. European Forest Research Institute Discussion Paper 13. Joensuu, Finland: European Forest Institute.

Desta, Z.A., Ortiz, R., 2014. Genomic selection: genome-wide prediction in plant improvement. Trends in Plant Science 19(9), 592-601. doi:10.1016/j.tplants.2014.05.006

Dislich, C., Keyel, A.C., Salecker, J., Kisel, Y., Meyer, K.M., Auliya, M., Barnes, A.D., Corre, M.D., Darras, K. , Faust, H., Hess, B., Klasen, S., Knohl, A., Kreft, H., Meijide, A., Nurdiansyah, F., Otten, F., Pe'er, G., Steinebach, S., Tarigan, S., Tölle, M.H., Tscharntke, T., Wiegand, K., 2017. A review of the ecosystem functions in oil palm plantations, using forests as a reference system. Biological Reviews 92(3), 1539-1569. doi:10.1111/brv.12295

Drössler, L., Övergaard, R., Ekö, P. M., Gemmel, P., Böhlenius, H., 2015. Early development of pure and mixed tree species plantations in Snogeholm, southern Sweden. Scandinavian Journal of Forest Research 30(4), 304-316. doi:10.1080/02827581.2015.1005127

Dyck, B., 2003. Benefits of planted forests: social, ecological and economic. Paper presented at the UNFF Intersessional Experts Meeting on the Role of Planted Forests in Sustainable Forest Management, Wellington, New Zealand. Retrieved from https://pdfs.semanticscholar.org/a32c/f4ec8b473f790428b76e80e629cd248b5766.pdf (July 25, 2017)

Erskine, P.D., Lamb, D., Bristow, M., 2006. Tree species diversity and ecosystem function: can tropical multi-species plantations generate greater productivity? Forest Ecology and Management 233(2-3), 205-210. doi:10.1016/j.foreco.2006.05.013

Evans, J., 2001. Biological sustainability of productivity in successive rotations (Working paper No. FP/2) (D. J. Mead, Ed.. Rome, Italy: FAO.

FACCE SURPLUS, 2016. SidaTim. Retrieved from http://faccesurplus.org/research-projects/sidatim (August 12, 2017)

FAO, 2001. Global Forest Resources Assessment 2000. FAO Forestry Paper 140. Rome, Italy: FAO.

FAO, 2006. Global Forest Resources Assessment 2005. FAO Forestry Paper 147. Rome, Italy: FAO.

FAO, 2010. Global Forest Resources Assessment 2010. FAO Forestry Paper 163. Rome, Italy: FAO.

Felton, A., Lindbladh, M., Brunet, J., Fritz, Ö., 2010. Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. Forest Ecology and Management 260(6), 939-947. doi:10.1016/j.foreco.2010.06.011

Felton, A., Nilsson, U., Sonesson, J., Felton, A. M., Roberge, J. M., Ranius, T., Ahlström, M., Bergh, J., Björkman, C., Boberg, J., Drössler, L., Fahlvik, N., Gong, P., Holmström, E., Keskitalo, E.C.H., Klapwijk, M.J., Laudon, H., Lundmark, T., Niklasson, M., Nordin, A., Pettersson, M., Stenlid, J., Sténs, A., Wallertz, K., 2016. Replacing monocultures with mixed-species stands: ecosystem service implications of two production forest alternatives in Sweden. Ambio 45(Suppl 2), 124-139. doi:10.1007/s13280-015-0749-2

Fischer, A., Vasseur, L., 2002. Smallholder perceptions of agroforestry projects in Panama. Agroforestry Systems 54(2), 103-113. doi:10.1023/A:1015047404867

Fjellstad, K. B., 2016. Establishment of high-productive mixtures. Retrieved from https://www.nordgen.org/en/establishment-high-productive-mixtures (April 2, 2018)

Forrester, D.I., Bauhus, J., Cowie, A.L., 2005. On the success and failure of mixed-species tree plantations: lessons learned from a model system of *Eucalyptus globulus* and *Acacia mearnsii*. Forest Ecology and Management 209(1-2), 147-155. doi:10.1016/j.foreco.2005.01.012

Forrester, D.I., Bauhus, J., Cowie, A.L., Vanclay, J.K., 2006. Mixed-species plantations of eucalyptus with nitrogen-fixing trees: a review. Forest Ecology and Management 233(2-3), 211-230. doi:10.1016/j.foreco.2006.05.012

Forrester, D.I., Theiveyanathan, S., Collopy, J.J., Marcar, N.E., 2010. Enhanced water use efficiency in a mixed *Eucalyptus globulus* and *Acacia mearnsii* plantation. Forest Ecology and Management 259(9), 1761-1770. doi:10.1016/j.foreco.2009.07.036

Francia, E., Tacconi, G., Crosatti, C., Barabaschi, D., Bulgarelli, D., Dall'Aglio, E., Vale, G., 2005. Marker assisted selection in crop plants. Plant Cell, Tissue and Organ Culture 82(3), 317-342. doi:10.1007/s11240-005-2387-z

Gebru, H., 2015. A review on the comparative advantages of intercropping to mono-cropping system. Journal of Biology, Agriculture and Healthcare, 5(9), 1-13.

Göltenboth, F., Hutter, C.P., 2004. New options for land rehabilitation and landscape ecology in Southeast Asia by "rainforestation farming". Journal for Nature Conservation 12(3), 181-189. doi:10.1016/j.jnc.2004.03.003

Govindaraj, M., Vetriventhan, M., Srinivasan, M., 2015. Importance of genetic diversity assessment in crop plants and its recent advances: an overview of its analytical perspectives. Genetics Research International 2015, Article ID 431487, 14 pages. doi:10.1155/2015/431487

Grattapaglia D., 2017. Status and perspectives of genomic selection in forest tree breeding. In: Sorrells, M.E. (ed) Genomic selection for crop improvement. Springer, Cham, pp 199–257.

Griess, V. C., Knoke, T., 2011. Growth performance, windthrow, and insects: meta-analyses of parameters influencing performance of mixed-species stands in boreal and northern temperate biomes. Canadian Journal of Forest Research 41(6), 1141-1159. doi:10.1139/x11-042

Gugerli, F., Englisch, T., Niklfeld, H., Tribsch, A., Mirek, Z., Ronikier, M., Zimmermann, N.E., Holderegger, R., Taberlet, P., IntraBioDiv Consortium, 2008. Relationships among levels of biodiversity and the relevance of intraspecific diversity in conservation—a project synopsis. Perspectives in Plant Ecology, Evolution and Systematics 10(4), 259-281. doi:10.1016/j.ppees.2008.07.001

Häggman, H., Sutela, S., Fladung, M., 2016. Genetic engineering contribution to forest tree breeding efforts. In C. Vettori, F. Gallardo, H. Häggman, V. Kazana, F. Migliacci, G. Pilate, and M. Fladung (Eds.), Biosafety of Forest Transgenic Trees, pp. 11-30. Dordrecht, Netherlands: Springer Science+Business Media.

Hamburdă, S.B., Munteanu, N., Teliban, G.C., 2015. Intercropping—a successful system for runner bean (*Phaseolus coccineus* L.) crop. Bulletin of University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca. Horticulture 72(1), 81-86. doi:10.15835/buasvmcn-hort:10453

Hamilton, A.J., 2005. Species diversity or biodiversity? Journal of Environmental Management, 75(1), 89-92. doi:10.1016/j.jenvman.2004.11.012

Harfouche, A., Meilan, R., Altman, A., 2011. Tree genetic engineering and applications to sustainable forestry and biomass production. Trends in Biotechnology 29(1), 9-17. doi:10.1016/j.tibtech.2010.09.003

Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. Forest Ecology and Management 155(1-3), 81-95. doi:10.1016/S0378-1127(01)00549-7

Humphrey, J.W., 2005. Benefits to biodiversity from developing old-growth conditions in British upland spruce plantations: a review and recommendations. Forestry 78(1), 33-53. doi:10.1093/forestry/cpi004

Iijima, M., Awala, S.K., Watanabe, Y., Kawato, Y., Fujioka, Y., Yamane, K., Wada, K.C., 2016. Mixed cropping has the potential to enhance flood tolerance of drought-adapted grain crops. Journal of Plant Physiology 192, 21-25. doi:10.1016/j.jplph.2016.01.004

IMPAC^3, 2014. Novel genotypes for mixed cropping allow for IMProved sustainable land use ACross arable land, grassland and woodland. Retrieved from https://www.uni-goettingen.de/en/543914.html (August 12, 2017)

Irwin, S., Pedley, S.M., Coote, L., Dietzsch, A.C., Wilson, M.W., Oxbrough, A., Sweeney, O., Moore, K.M., Martin, R., Kelly, D.L., Mitchell, F.J.G., Kelly, T.C., O'Halloran, J., 2014. The value of plantation forests for plant, invertebrate and bird diversity and the potential for cross-taxon surrogacy. Biodiversity and Conservation 23(3), 697-714. doi:10.1007/s10531-014-0627-4

Iwata, H., Minamikawa, M.F., Kajiya-Kanegae, H., Ishimori, M., Hayashi, T., 2016. Genomics-assisted breeding in fruit trees. Breeding Science 66, 100–115. doi:10.1270/jsbbs.66.100

Jing, J., Søegaard, K., Cong, W. F., Eriksen, J., 2017. Species diversity effects on productivity, persistence and quality of multispecies swards in a four-year experiment. PloS one 12(1), e0169208. doi:10.1371/journal.pone.0169208

Jonas, E., Fikse, F., Rönnegård, L., Mouresan, E.F., 2018. Genomic Selection. In: Population Genomics. Springer, Cham. doi:10.1007/13836_2018_11

Jose, S., 2009. Agroforestry for ecosystem services and environmental benefits: an overview. Agroforestry Systems 76(1), 1-10. doi:10.1007/s10457-009-9229-7

Jürgensen, C., Kollert, W., Lebedys, A., 2014. Assessment of industrial roundwood production from planted forests. FAO Planted Forests and Trees Working Paper FP/48/E. Rome, Italy: FAO.

Kanninen, M., 2010. Plantation forests: global perspectives. In J. Bauhus, P. van der Meer, M. Kanninen (Eds.), Ecosystem Goods and Services from Plantation Forests, pp. 1-15. London, UK: Earthscan.

Kanowski, J., Catterall, C.P., Wardell-Johnson, G.W., 2005. Consequences of broadscale timber plantations for biodiversity in cleared rainforest landscapes of tropical and subtropical Australia. Forest Ecology and Management 208(1-3), 359-372. doi:10.1016/j.foreco.2005.01.018

Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., ...Wirth, C., 2011. TRY—a global database of plant traits. Global Change Biology 17(9), 2905-2935. doi:10.1111/j.1365-2486.2011.02451.x

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A., Lindquist, E., 2015. Dynamics of global forest area: results from the FAO Global Forest Resources Assessment 2015. Forest Ecology and Management 352, 9-20. doi:10.1016/j.foreco.2015.06.014

Kelty, M.J., 2006. The role of species mixtures in plantation forestry. Forest Ecology and Management 233(2-3), 195-204. doi:10.1016/j.foreco.2006.05.011

Kuchma, O., Ropertz, J., Leinemann, L., Krutovsky, K., 2017. Transcriptome analysis of poplar clones to understand differences in their genetic performance in pure and mixed stand with black locust. Poster session presented at the PLANT 2030 Status Seminar 2017, Potsdam, Germany.

Larjavaara, M., 2008. A review on benefits and disadvantages of tree diversity. Open Forest Science Journal 1, 24-26.

Lefcheck, J.S., Byrnes, J.E., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N., Hensel, M.J.S., Hector, A., Cardinale, B.J., Duffy, J. E., 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nature Communications 6, 6936. doi:10.1038/ncomms7936

Li, Y., Chen, X., Xie, Y., Li, X., Li, F., Hou, Z., 2014. Effects of young poplar plantations on understory plant diversity in the Dongting Lake wetlands, China. Scientific Reports 4, 6339. doi:10.1038/srep06339

Lin, Z., Hayes B.J., Daetwyler H.D., 2014. Genomic selection in crops, trees and forages: a review. Crop Pasture Sci. 65: 1177–1191.

Lohbeck, M., Bongers, F., Martinez-Ramos, M., Poorter, L., 2016. The importance of biodiversity and dominance for multiple ecosystem functions in a human-modified tropical landscape. Ecology 97(10), 2772-2779. doi:10.1002/ecy.1499

Mace, G. M., Norris, K., Fitter, A. H., 2012. Biodiversity and ecosystem services: a multilayered relationship. Trends in Ecology and Evolution 27(1), 19-26. doi:10.1016/j.tree.2011.08.006

Malézieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Ozier-Lafontaine, H., Rapidel, B., de Tourdonnet, S., Valantin-Morison, M., 2009. Mixing plant species in cropping systems: concepts, tools and models: A review. Agronomy for Sustainable Development 29(1), 43-62. doi:10.1051/agro:2007057

Manson, D.G., Schmidt, S., Bristow, M., Erskine, P. D., Vanclay, J.K., 2013. Species-site matching in mixed species plantations of native trees in tropical Australia. Agroforestry Systems 87(1), 233-250. doi:10.1007/s10457-012-9538-0

Mergeay, J., Santamaria, L., 2012. Evolution and biodiversity: the evolutionary basis of biodiversity and its potential for adaptation to global change. Evolutionary Applications 5(2), 103-106. doi:10.1111/j.1752-4571.2011.00232.x

Minhas, P.S., Yadav, R.K., Lal, K., Chaturvedi, R.K., 2015. Effect of long-term irrigation with wastewater on growth, biomass production and water use by eucalyptus (*Eucalyptus tereticornis* Sm.) planted at variable stocking density. Agricultural Water Management 152, 151-160. doi:10.1016/j.agwat.2015.01.009

Moghaddam, E.R., 2014. Growth, development and yield in pure and mixed forest stands. International Journal of Advanced Biological and Biomedical Research 2(10), 2725-2730.

Montagnini, F., Cusack, D., Petit, B., Kanninen, M., 2004. Environmental services of native tree plantations and agroforestry systems in Central America. Journal of Sustainable Forestry 21(1), 51-67. doi:10.1300/J091v21n01_03

Moose, S.P., Mumm, R.H., 2008. Molecular plant breeding as the foundation for 21st century crop improvement. Plant Physiology 147(3), 969-977. doi:10.1104/pp.108.118232

Morris, J., Ningnan, Z., Zengjiang, Y., Collopy, J., Daping, X., 2004. Water use by fast-growing *Eucalyptus urophylla* plantations in southern China. Tree Physiology 24(9), 1035-1044. doi:10.1093/treephys/24.9.1035

Mosquera-Losada, M.R., McAdam, J.H., Romero-Franco, R., Santiago-Freijanes, J.J., Rigueiro-Rodróguez, A., 2009. Definitions and components of agroforestry practices in Europe. In A. Rigueiro-Rodróguez, J. McAdam, and M. R. Mosquera-Losada (Eds.), Agroforestry in Europe, pp. 3-19. Dordrecht, Netherlands: Springer Science+Business Media.

Mutanal, S.M., Patil, S.J., Shahapurmath, G., 2007. Studies on mixed cropping of tree species with tamarind (*Tamarindus indica*). Karnataka Journal of Agricultural Sciences 20(3), 568-570.

Nambiar, E.S., 1999. Productivity and sustainability of plantation forests. Bosque 20(1), 9-21.

Nerlich, K., Graeff-Hönninger, S., Claupein, W., 2013. Agroforestry in Europe: a review of the disappearance of traditional systems and development of modern agroforestry practices, with emphasis on experiences in Germany. Agroforestry Systems 87(2), 475-492. doi:10.1007/s10457-012-9560-2

Newell, M.A., Jannink, J.L., 2014. Genomic selection in plant breeding. Methods in Molecular Biology 1145, 117-130. doi:10.1007/978-1-4939-0446-4_10

Nghiem, N., Tran, H., 2016. The biodiversity benefits and opportunity costs of plantation forest management: a modelling case study of *Pinus radiata* in New Zealand. Forests 7(12), 297. doi:10.3390/f7120297

Nguyen, H., Firn, J., Lamb, D., Herbohn, J., 2014. Wood density: A tool to find complementary species for the design of mixed species plantations. Forest Ecology and Management 334, 106-113. doi:10.1016/j.foreco.2014.08.022

Nguyen, H., Herbohn, J.L., Clendenning, J., Lamb, D., Dressler, W., Vanclay, J.K., Firn, J., 2015. What is the available evidence concerning relative performance of different designs of mixed-species plantings for smallholder and community forestry in the tropics? A systematic map protocol. Environmental Evidence 4(15), 1-7. doi:10.1186/s13750-015-0041-8

Nichols, J.D., Bristow, M., Vanclay, J.K., 2006. Mixed-species plantations: prospects and challenges. Forest Ecology and Management 233(2-3), 383-390. doi:10.1016/j.foreco.2006.07.018

Paquette, A., Messier, C., 2010. The role of plantations in managing the world's forests in the Anthropocene. Frontiers in Ecology and the Environment 8(1), 27-34. doi:10.1890/080116

Parrotta, J.A., 1999. Productivity, nutrient cycling, and succession in single-and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. Forest Ecology and Management 124(1), 45-77. doi:10.1016/S0378-1127(99)00049-3

Pawson, S.M., Brin, A., Brockerhoff, E.G., Lamb, D., Payn, T.W., Paquette, A., Parrotta, J.A., 2013. Plantation forests, climate change and biodiversity. Biodiversity and Conservation 22(5), 1203-1227. doi:10.1007/s10531-013-0458-8

Payn, T., Carnus, J.M., Freer-Smith, P., Kimberley, M., Kollert, W., Liu, S., Orazio, C., Rodriguez, L., Silva, L.N., Wingfield, M.J., 2015. Changes in planted forests and future global implications. Forest Ecology and Management 352, 57-67. doi:10.1016/j.foreco.2015.06.021

Pelleri, F., Ravagni, S., Bianchetto, E., Bidini, C., 2013. Comparing growth rate in a mixed plantation (walnut, poplar and nurse trees) with different planting designs: results from an experimental plantation in northern Italy. Annals of Silvicultural Research 37(1), 13-21.

Pereira, H.M., Navarro, L.M., Martins, I.S., 2012. Global biodiversity change: the bad, the good, and the unknown. Annual Review of Environment and Resources 37, 25-50.

Petit, B., Montagnini, F., 2006. Growth in pure and mixed plantations of tree species used in reforesting rural areas of the humid region of Costa Rica, Central America. Forest Ecology and Management 233(2-3), 338-343. doi:10.1016/j.foreco.2006.05.030

Piotto, D., 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. Forest Ecology and Management *255*(3-4), 781-786. doi:10.1016/j.foreco.2007.09.065

Plath, M., Mody, K., Potvin, C., Dorn, S., 2011. Establishment of native tropical timber trees in monoculture and mixed-species plantations: small-scale effects on tree performance and insect herbivory. Forest Ecology and Management 261(3), 741-750. doi:10.1016/j.foreco.2010.12.004

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology and Evolution 25(6), 345-353. doi:10.1016/j.tree.2010.01.007

Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. Forest Ecology and Management 327, 251-264. doi:10.1016/j.foreco.2014.04.027

Pretzsch, H., Rötzer, T., Schütze, G., Schäfer, C., 2014. Tree and stand-level growth reactions on drought in mixed versus pure forests of Norway spruce and European beech. Retrieved from http://kroof.wzw.tum.de/index.php?id=13&L=1 (August 12, 2017)

Pretzsch, H., Schütze, G., 2016. Effect of tree species mixing on the size structure, density, and yield of forest stands. European Journal of Forest Research 135(1), 1-22. doi:10.1007/s10342-015-0913-z

Richards, A.E., Forrester, D.I., Bauhus, J., Scherer-Lorenzen, M., 2010. The influence of mixed tree plantations on the nutrition of individual species: a review. Tree Physiology 30(9), 1192-1208. doi:10.1093/treephys/tpq035

Schneider, F.D., Brose, U., Rall, B.C., Guill, C., 2016. Animal diversity and ecosystem functioning in dynamic food webs. Nature Communications 7, 12718. doi:10.1038/ncomms12718

Schuler, L.J., Bugmann, H., Snell, R.S., 2017. From monocultures to mixed-species forests: is tree diversity key for providing ecosystem services at the landscape scale? Landscape Ecology 32(7), 1499-1516. doi:10.1007/s10980-016-0422-6

Sedjo, R.A., 1999. The potential of high-yield plantation forestry for meeting timber needs. New Forests 17(1-3), 339-360. doi:10.1023/A:1006563420947

Sedjo, R.A., 2001. The role of forest plantations in the world's future timber supply. The Forestry Chronicle 77(2), 221-225.

Shelton, S., 2012. Restoring a 'Wonder Tree' in a Changing Climate. Retrieved from https://www.fws.gov/endangered/map/ESA_success_stories/GA/GA_story1/index.html (August 2, 2017)

Smith, J., 2010a. Agroforestry: reconciling production with protection of the environment a synopsis of research literature. The Organic Research Centre, Elm Farm, Hamstead Marshall, Newbury, Berkshire. Retrieved from http://orgprints.org/18172/1/Agroforestry_synopsis.pdf (August 6, 2017)

Smith, J., 2010b. The history of temperate agroforestry. The Organic Research Centre, Elm Farm, Hamstead Marshall, Newbury, Berkshire. Retrieved from http://orgprints.org/18173/1/History_of_agroforestry_v1.0.pdf (August 6, 2017)

Songstad, D.D., Petolino, J.F., Voytas, D.F., Reichert, N.A., 2017. Genome editing of plants. Critical Reviews in Plant Sciences, 36(1), 1-23. doi:10.1080/07352689.2017.1281663

Srivastava, D.S., Vellend, M., 2005. Biodiversity-ecosystem function research: is it relevant to conservation? Annual Review of Ecology, Evolution, and Systematics 36, 267-294.

Subasinghe, K., Sumanapala, A.P., Weerawardhena, S.R., 2014. The impact of forest conversion on bird communities in the northern flank of the Knuckles Mountain Forest Range, Sri Lanka. Journal of Asia-Pacific Biodiversity 7(4), 367-373. doi:10.1016/j.japb.2014.07.004

Swift, M.J., Izac, A.M., van Noordwijk, M., 2004. Biodiversity and ecosystem services in agricultural landscapes—are we asking the right questions? Agriculture, Ecosystems and Environment, 104(1), 113-134. doi:10.1016/j.agee.2004.01.013

Thomsen, I.M., 2016. Mixed forests and fungal diseases: potential solutions or problems? Abstract of the paper presented at the NordGen Forest Conference, Växjö, Sweden. Retrieved from https://www.nordgen.org/ngdoc/forest/Konferanser/2016/Abstracts.pdf (August 1, 2017)

Thünen-Institut, 2014. Maize and beans in mixed cropping. Retrieved from https://www.thuenen.de/en/ol/projects/by-specialist-disciplines/crop-and-fodder-production/maize-and-beans-in-mixed-cropping (August 12, 2017)

Tilman, D., Reich, P. B., Knops, J. M., 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441(7093), 629-632. doi:10.1038/nature04742

Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379(6567), 718-720. doi:10.1038/379718a0

Weigelt, A., Weisser, W.W., Buchmann, N., Scherer-Lorenzen, M., 2009. Biodiversity for multifunctional grasslands: equal productivity in high-diversity low-input and low-diversity high-input systems. Biogeosciences 6(8), 1695-1706.

West, P.W., 2014. Growing plantation forests. Cham, Switzerland: Springer International Publishing.

Williams, J., 2001. Financial and other incentives for plantation establishment. Working paper No. FP/8, D.J. Mead, Ed. Rome, Italy: FAO.

Wilson, M.H., Lovell, S.T., 2016. Agroforestry—the next step in sustainable and resilient agriculture. Sustainability 8(6), 574. doi:10.3390/su8060574

WORLD COFFEE RESEARCH, 2017. Breeding for climate change. Retrieved from https://worldcoffeeresearch.org/news/breeding-climate-change (August 12, 2017)

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314(5800), 787-790. doi:10.1126/science.1132294

Yadav, S.K., Mishra, G.C., 2013. Biodiversity measurement determines stability of ecosystems. International Journal of Environmental Science: Development and Monitoring 4, 68-72.

Zhai, M., Jiang, S., Jia, L., 2006. Nutrient dynamics of fine roots in the mixed plantation of poplar and black locust. Frontiers of Forestry in China 1(1), 70-75. doi:10.1007/s11461-005-0008-y

Zhang, Y., Chen, H.Y., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. Journal of Ecology 100(3), 742-749. doi:10.1111/j.1365-2745.2011.01944.x

Zhao, H., Yang, W., Wu, F., Tan, B., 2017. Mixed forest plantations can efficiently filter rainfall deposits of sulfur and chlorine in Western China. Scientific Reports 7, 41680. doi:10.1038/srep41680