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Review Article

Growth, Development and Yield in Pure and Mixed Forest Stands

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ABSTRACT

Objective: Ecosystems with mixed species compared to the ones with pure compositions provide a broader range of options in the fields of biodiversity, conservation, protection and restoration. Nearly all forest plantations are established as monocultures, but research has shown that there are potential advantages to be gained by using carefully designed species mixtures in place of monocultures. This paper reviews recent studies that compare stand development and productivity of mixed and pure plantations. **Results:** Higher stand-level productivity in mixtures has been found with species interactions. These mixtures can also improve economic return through greater individual-tree growth rates and provision of multiple commercial or subsistence products. More complex plantation mixtures of several species have been used for ecological restoration of degraded lands; these large numbers of species of different successional stages are combined to reduce the need for a series of sequential plantings. Future research needs to examine many more tree species across a wider range of sites.

INTRODUCTION

Forest plantations are being established at an increasing rate throughout much of the world, and now account for 5% of global forest cover (FAO, 2001). In forestry, the importance of mixed stands has increased in recent decades due to the potential benefits which can be gained, such as increased production, greater diversity, improved nutrient cycling or reduced risk of biotic and abiotic damage. The question of potential productivity in mixed as opposed to pure stands has long been an area of interest in forest research although there is a lack of general approaches for studying this topic (Rio and Sterba, 2009). Thus, the papers in this issue deal with a very small segment of the world's plantations, so it is reasonable for proponents of mixed-species plantations to be asked, ''Why mixtures?'' As a prelude to presenting an answer, it is logical to first review the reasons for the dominant practice, and ask, ''Why monocultures?'' A principal advantage of monocultures over mixed-species forests is the ability to concentrate all site resources on the growth of a species with the most desirable characteristics, generally relating to growth rate and wood quality. In addition, the simplicity of stand management is of great importance. There are substantial economic benefits to be gained from using simple, standardized silviculture and harvest operations that produce uniform products (Evans and Turnbull, 2004). The same is true of the simplicity of nursery practice when working with one or a very few species. Returning to the initial question regarding the reasons for studying mixed-species plantations, the objective of much of the research is to examine whether mixtures can provide greater yields or other benefits than monocultures at a level that may outweigh the advantages of management simplicity. Much of the interest among researchers is in mixtures of 2, 3, or 4 tree species. These are the types most likely to substitute for monocultures where wood production is the main objective. The goal is to combine particular species to

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produce specific interactions that will increase stand-level productivity or individual-tree growth rates relative to monocultures, allow harvest products from different species on different rotations, reduce risk of market shifts or insect or disease impacts, or achieve some combination of these. There is also interest in using mixed-species plantations in ecological restoration of degraded land; these are composed of a moderate to very large number of planted species in order to directly reestablish part of the native diversity of tree vegetation, and to foster the establishment of additional native plant species in the plantation understory.

This paper briefly reviews the principal lines of research examining the various uses of mixtures, and presents some examples of these recent experiments and operational applications; the papers in this special issue then expand further on many of the topics. This paper is not intended to be a comprehensive review; specific aspects have been reviewed in greater depth elsewhere (Cannell et al., 1992; Kelty, 1992; Wormald, 1992; Rothe and Binkley, 2001; Forrester et al., 2005; Lamb et al., 2005; Rouhi-Moghaddam et al., 2008a; Rio and Sterba, 2009). The paper is organized by the various objectives associated with the management of plantation mixtures, with some suggestions for future research at the conclusion.

Increasing stand-level productivity using complementary characteristics

High stand-level productivity is clearly an important characteristic for wood production, and it is also associated with carbon and other nutrient sequestration objectives. A key concept for designing highly productive mixed-species stands is the need to combine species that differ in characteristics such as shade tolerance, height growth rate, crown structure (particularly leaf area density), foliar phenology (particularly deciduous versus evergreen habit), and root depth and phenology (Kelty, 1992). If the species differ substantially in these characteristics, they may capture site resources more completely and/or use the resources more efficiently in producing biomass, resulting in greater total stand biomass production than would occur in monocultures of the component species. Such species are said to have complementary resource use (Haggar and Ewel, 1997) or good ecological combining ability (Harper, 1977). This interaction is often described in terms of competition intensity. Two species with similar growth characteristics have interspecific competition in mixture that is equal to that of intraspecific competition in monoculture. Species with complementary characteristics have interspecific competition that is much lower than intraspecific. For that reason, the phenomenon of higher production from this type of interaction is also called the competitive production principle (Vandermeer, 1989). The relationship between juvenile height growth rate and degree of shade tolerance plays an important role in mixed plantations (Menalled et al., 1998). In general, intolerant species grow rapidly in height, allocate more growth to stem and branches, and have crowns with low leaf area density (Haggar and Ewel, 1995; Canham et al., 1994; Sheil et al., 2006; Hosseini et al., 2010). These species can form an upper canopy stratum that transmits a substantial portion of light to shade tolerant species that form a lower stratum with greater leaf area density. Canopy stratification of this kind is an important aspect of complementary resource use. Root stratification may also occur, but there is much less information about below ground processes. In species combinations where complementarity of crown or root structure is an important interaction, a fine-grained spatial pattern (i.e., with the species intermixed on a tree-by-tree basis) is necessary to maximize interspecific interactions. The proportions of the species in mixtures can have important effects on stand development. Several studies have tested the question of whether biomass productivity in mixed plantations with complementary characteristics exceeds that in monocultures of the component species (Amoroso and Turnblom, 2006).

Increasing stand-level productivity using facilitation

Much more research has been focused on mixed-species plantations designed to produce facilitative interactions than those designed solely for complementarity of resource use (e.g., Forrester et al., 2006a; Hosseini et al., 2008; Hosseini et al., 2011a; Rouhi-Moghaddam et al., 2011a). The facilitative production principle (Vandermeer, 1989) involves one species directly benefiting the growth of another. The greatest use of facilitation in forest plantations has been through the combination of an N-fixing tree species (those with root symbionts that fix atmospheric N2) and a non-N-fixing, valuable timber tree species that shows substantial growth responses to increased N availability. The species are grown in mixture to allow N to be transferred from the N-fixing species to the companion species. The more rapid nutrient cycling of the N-rich litter may increase available pools of other nutrients as well, but in some cases available P has been found to decrease, due apparently to the high demand for P by some Nfixing species (Rothe and Binkley, 2001). With some species combinations, there may also be a more direct transfer of N and other nutrients between trees species through an ectomycorrhizal connection if the tree species share the same ectomycorrhizal species (Simard et al., 1997; Rachid et al., 2013).

Although most experimental plantings have been conducted on just a single site, there is evidence from some studies that facilitative interactions do not produce greater biomass in mixtures on sites with high N availability. These studies included manipulations of nutrient levels for small groups of trees growing in pots (Forrester et al., 2006b) and field studies on multiple sites (Binkley, 2003; Boyden et al., 2005; Rouhi-Moghaddam et al., 2012). There is also considerable interest in using facilitative interactions to improve tree nutrition with combinations of species that do not include an N-fixing species. A common practice in European forestry is to mix a broadleaf tree species with a valuable conifer species with one objective being to increase the rate of nutrient cycling (Matthews, 1989).

Improving individual-tree growth rate and stem quality

The size and allometry of trees in monoculture stands are strongly affected by stand density, through its influence on the intensity of intraspecific competition. Plantations are generally established at densities that are high enough to cause shading of lower branches and thus improve stem quality in the early stage of stand development. Silviculturists then have the option of maintaining high density for maximum stand-level production or reducing density substantially to promote individual tree growth. Mixed-species plantations with stratified canopies can provide an advantage in this regard. Initial planting densities can be as high as in monocultures, but then the effective density (in terms of crown competition) will begin to decline as canopy stratification develops. Crown and stem size may increase relative to trees in monoculture of the same initial density. The species of the upper canopy would be more likely to develop larger stems; the crowns of lower canopy species may expand laterally, but their overall growth rate would be affected by their shade tolerance as well as the density of upper canopy. The effect on growth increases of upper canopy species would be exaggerated by reducing the initial planting density of that species. Larger individual tree sizes of one or both species in mixed stands compared to monocultures were found in several experimental stands described (Rouhi-Moghaddam et al., 2009; Verónica Loewe et al., 2013). Stratified mixtures can also promote stem quality of the upper canopy species. For example, the valuable timber species Quercus petraea is commonly grown in mixture with Fagus sylvatica in France and Germany (Matthews, 1989) so that the crowns of the lower canopy F. sylvatica will shade any epicormic branches that develop on the Q. petraea stems. However, mixtures can create stem quality problems if the difference in juvenile height growth rate between the species is too great.

Growing multiple products on varying rotations

One advantage of mixed-species plantations is that market risk may be reduced by growing a variety of products. This involves the usual tradeoffs inherent in predicting markets with the option of putting all resources into the single product that has highest value at present, or diversifying production; of course, the diversification option will not always give the highest return. There may also be a more predictable advantage for mixtures in the timing of production of commercial or subsistence products. Generally, the largest financial problem that forest landowners face when establishing plantations is the length of time from the large initial investment of site preparation, planting, and control of competing vegetation to the economic return in forest products at the end of the rotation.

Reducing risk of pest damage

One desired benefit of using species mixtures is a reduction of insect or disease damage. Much of the research that does focus on pest effects compares monocultures to complex natural forests (e.g., Jactel et al., 2002). Many potential managers of mixed-species plantations would be interested in whether only 2, 3, or 4 species in mixture reduce risk compared to monocultures, and there is very little information about these low-diversity mixtures. The potential risk of monocultures is that the invasion of a pest would affect all or most of the trees because of the uniform genetic composition. Recent reviews on the vulnerability of plantations (Powers, 1999; Gadgil and Bain, 1999) noted that most plantations (which are nearly all monocultures) have low incidences of insect and disease problems. Two mechanisms by which mixtures may reduce risk of pest damage are: (1) mixtures may dilute the host concentration for a pest organism and thereby impair the ability of the pest to find the host; (2) mixtures may provide more diverse habitats that tend to support higher populations of natural enemies of the pest species (Watt, 1992).

Restoring degraded lands

Mixed-species plantations potentially have a very different role to play compared to objectives described above as a part of the restoration of degraded lands. Tree planting has long been used as part of the reclamation of mining spoils; for example, a legal requirement that Alnus spp. be planted on abandoned coal mines was established in Germany in 1766 (Lo¨gters and Dworschak, 2004). Early research focused on the selection of species for their ability to withstand difficult site conditions (e.g., low pH and organic matter, and high levels of certain elements). Species trials were often planted as mixtures, and this kind of planting became operational in many cases. Much of the goal was simply to vegetate the site in order to reduce erosion. A good deal of recent research on the restoration of abandoned agricultural lands has been devoted to evaluations of commercial timber plantations (generally monocultures of nonnative species) as initiators of forest succession (Parrotta et al., 1997; Hosseini et al., 2011b). These plantations act as nurse trees to shade out grasses and other post-agricultural vegetation, and provide a forest habitat structure that attracts animal dispersers of many native plant species. It has been proposed that the restoration of highly structured and diverse forest plant communities must involve sequential introductions of species of different characteristics or stages of succession, as opposed to simultaneous introductions in a mixed planting (Dobson et al., 1997; Rouhi-Moghaddam et al., 2007, 2011b; 2011c).

Expanding the information base for designing mixtures

The results of recent studies (those reviewed here, and others) have substantially increased our knowledge base on the development and production of mixed-species plantations. However, there still has been little work on a number of aspects of the topic: the prevalence and mechanisms of beneficial below ground interactions; the effects of site factors and spacing on species interactions; and the prevalence of beneficial interactions across a broad range of tree species. Experiments on the mechanisms of interactions among species are so expensive that most are carried out on very small plots, nearly all are on one site type and at one spacing level, and only a small number of tree species have been included. Most studies have used replacement series designs, which focus on variations of species proportions at a constant overall spacing (Sackville Hamilton, 1994; Kelty and Cameron, 1995; Rouhi-Moghaddam et al., 2008b). Some also include additive series to incorporate variation in spacing, and some include both synchronous and delayed planting, where one species has a very rapid juvenile growth rate. However, it is unlikely that funding will be available to expand many replicated replacement/additive experiments to include all these important factors.

CONCLUSION

When timber production is the primary objective of management, there is a clear tendency to favor monocultures of the most productive species. This is mainly because of the simpler management of monocultures (easier and cheaper establishment, planning and marketing), but also, though no less important, because less is known about planted mixed stands and the interactions between species. In contrast, when mixed-species stands are favored, the objectives usually include wildlife conservation, aesthetics, resistance to wind damage, risk reduction or compensatory growth, and protection from disease and insect outbreaks. A sacrifice in productivity, compared to the most productive species, is usually assumed to occur as a consequence of the use of mixed-species stands (Amoroso and Turnblom, 2006). Ecological theory suggests that species in a mixture may exploit resources of a site more completely and efficiently than a single species would be able to do, leading to greater overall productivity. Even though this has been observed in many situations, it is not always likely to happen. To achieve greater productivity in mixed stands, the species constituting the stands need to show differences in their requirements (niches) and the way they use site resources and (or) positively affect the growth of each other. This concept of niche separation implies that if two species are too similar in their requirements they would eventually compete intensely to exclude the other, but if competition is sufficiently weak, the two species may coexist (Harper, 1977).

In mixtures, inter-specific competition may be less than intra-specific competition. Moreover, in mixed-species plantations, some species, such as the legumes, may nurse adjacent trees and/or species of trees. Larger tree species can provide needed shelter for more slow-growing species and intercept potential pests (Amoroso and Turnblom, 2006; Petit and Montagnini, 2006). Within the community of mixed-species researchers, it is easy to gain the impression that there is widespread support and demand for mixed-species plantations, but this is not generally so in the case of commercial plantations for timber production (Nichols et al. 2006).

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