The Development of Mixed Species Plantations as Successional Analogues to Natural Forests

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Abstract -Moist temperate and tropical forests often regenerate after disturbance regimes (hurricanes, tree falls, pathogens) that promote allogenic processes (initial floristics) of stand development. Disturbance regimes that are more lethal to advance regeneration, such as land clearance for agriculture and subsequent abandonment, promote autogenic processes (relay floristics) of stand development. We propose models for development of mixed plantations that reflect these successional patterns. Initial findings from experiments adopting guidelines that carefully consider the spatial arrangement and timing of mixed plantings can promote the inclusion of late-successional canopy timber species with subcanopy species that provide non-timber forest products (latex, spices, medicinal herbs, fruits). Past experiments have demonstrated poor establishment of subcanopy and late-seral tree species when planted as a single species in open conditions.

We propose experimental mixed plantations that aim to reflect the stand dynamics of natural forests. Using the stand development paradigm of Oliver and Larson (1990) the initiation phase of stand development is represented by the nurse stage of plantation establishment, the stem exclusion phase is reflected during the training period of plantation growth, and the understory initiation and old growth phases can be equated with the tree and crop harvest period at the end of a plantation's rotation. The establishment of experimental mixed plantings requires careful choice for species that are site-specific, shade-tolerant and late-successional. Planted on an appropriate site experiments need to test their survival and establishment within a compatible matrix of faster-growing pioneers that provide partial shade. Preliminary results have shown that initial spacing and differential growth rates can accentuate dynamic canopy stratification. Under-planting trees and shrubs normally of the forest subcanopy can create a more static structural stratification that can increase economic value through yield of non-timber forest products, increase net primary productivity, and enhance wildlife habitat characteristics.

INTRODUCTION

In this paper we first describe the patterns and processes that facilitate the growth of species as compatible mixtures in moist temperate and tropical forests. We then provide a rationale for their simplistic reconstruction as plantation analogues on abandoned agricultural lands. Lastly this paper describes models for potential testing and development of mixed plantations and provides preliminary information on experiments that have established them based on our knowledge of moist forest dynamics.

Many studies have documented tree species mixtures to be stratified both over time and in vertical space for natural forests of moist temperate and tropical climates. In these regions soils are moist enough during the growing season to reduce the importance of water acquisition by the plant roots as a limiting process. This has promoted the expansion of below canopy environments within which shade tolerant plants can grow and survive. The complexity of vertical stratification is largely limited by the degree to which the availability of water and other edaphic resources to the roots limits the ability of the plant to allocate resources for light capture. The degree of vertical complexity in stratification varies at resource scales that are often based on light-water interactions. Such changes can be seen primarily between different topographic sites within a watershed such as between ridge and valley, or between different soil or geological types such as between a shallow till and deep outwash. Other examples of complexity change can be observed across more regional, physiographically based landscapes, for example between the leeward and windward sides of a mountain range, or between northern and southern aspects of mountain slopes. Watershed influences on vertical canopy stratification can largely be attributed to below-ground differences in the nature of hydrological flow pathways and storage, and entrained flows and deposition of nutrients and soil structural components. Regional physiographic influences on vertical canopy stratification are often associated with climatic differences in precipitation or incident radiation, but may also be associated with changing water or nutrient availability due to differing parent material of the soil or dominant surficial geology.

Conceptually, stratification can be characterized in two modes: dynamic and static. Both exist and occur together but vary in their importance depending on the nature and disturbance history of the site. Dynamic stratification can be described as that part of vertical complexity of forest stand structure that is most closely associated with succession. Tree species considered fast-growing pioneers are overtopped by slower-growing but eventually taller and longer-lived tree species. This process has been described as having several phases of stand development which closely parallel changes in the resource use efficiency and therefore the competitive ability of trees to grow and develop (Figure 1). Based primarily on North American literature four phases of development have been proposed by Oliver and Larson (1990). The initiation phase can be considered the first developmental stage of stand reorganization, regeneration site colonization and/or release after disturbance.

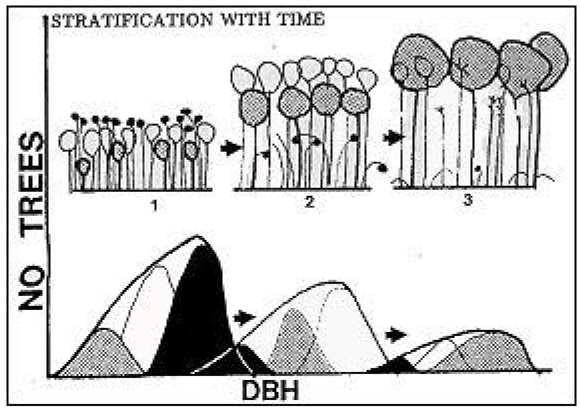

Figure 1. A hypothetical diagram depicting diameter distribution and associated dynamic canopy stratification of an even-aged cohort of mixed-species over different phases of stand development (early successional (1); mid successional (2); Late-successional (3)). The different shading represents different species crown positions and diameter distributions over time.

The stem exclusion phase follows this period and can be regarded as the most active post-establishment period of sorting and self-thinning with growing space totally occupied by the stand. A stand enters into the understory initiation phase of stand development when the maintenance of larger canopy tree sizes promotes less efficient capture and use of resources, and therefore makes growing space available for the re-initiation of groundstory advance regeneration and other often herbaceous plants. This phase also occurs when an increase in the spatial scale of canopy gaps, caused either by increasing tree size or by partial disturbance, exceeds the declining ability of the large canopy trees to reoccupy vacant growing space. The old growth phase is the last period of stand development. Here, the process of understory re-initiation has progressed enough to promote irregular canopy tree death and subsequent patchy release of the groundstory that eventually develops an all-aged tree canopy.

A similar stand development paradigm has been described in the European and old world tropical literature (Watt 1947). Gap phase can be equated to stand initiation; building phase to stem exclusion; and mature phase to the combination of understory re-initiation and old growth. Examples of dynamic stratification of tree mixtures have been reported for birch, oak, maple forests of southern New England (Oliver and Stephens 1977; Oliver 1978); bottomland hardwood of the southern U.S. (Clatterbuck et al. 1987; Oliver et al. 1989); piedmont hardwoods of the Carolinas' (O'Hara 1986); spruce-aspen of the north central states and Canada (Palik & Pregitzer 1993) and coniferous mixtures of the coastal northwest (Stubblefield & Oliver 1978; Wierman & Oliver 1977). The moist tropics have been similarly described particularly with mixtures in the neotropics of central and south America (Uhl et al. 1981; Brokaw 1985; Uhl et al. 1988), and old world tropics of southeast Asia and west Africa (Whitmore 1984; Swaine & Hall 1988; Swaine & Whitmore 1988).

Static stratification can be described as that part of vertical complexity of the forest stand that promotes the permanent existence of a subcanopy and groundstory comprised of plants that never succeed to the canopy. This pattern is most characteristic of moist forest regions with long-term disturbance intervals that allow for the progressive accentuation of vertical habitat strata. Examples of this kind of stratification have been well described in the classical tropical literature (Davis & Richards 1933, 1934; Beard 1944; Black et al. 1950; Ashton 1964; Whitmore 1974). A simple type of static stratification has been described for the southern boreal forest (Cooper 1913; 1928). Many of the more complex temperate forests also have well defined strata particularly in the wet coastal Pacific northwest (Wierman & Oliver 1977) and the cove forests of the southern Appalachians (Braun 1942; Lorimer 1980) (Figure 2).

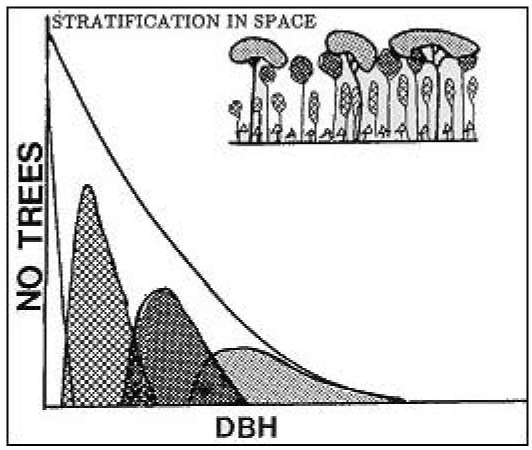

Figure 2. A hypothetical diagram depicting diameter distribution and associated canopy stratification of an even-aged cohort of mixed-species that permanently occupy different canopy strata over time.

The description of this type of stratification as static is largely one of temporal perspective; some static stratification patterns, such as those of the boreal forest, may be dependent on severe disturbance for long-term maintenance at the landscape scale.

Intermediate between these two types of stratification are examples of long-lived canopy trees that eventually relinquish their canopy space to subcanopy trees that are still longer-lived through gradual canopy disturbances such as ice storms and branch breakage from winds. Depending on the time scale of stand development this can almost be interpreted as part of static forest stratification rather than the last part of dynamic stratification. These intermediate descriptions of forest stratification have been documented for southern New England for hemlock beneath oak (Kelty 1986), and for white oak beneath tulip poplar (O'Hara 1986).

The diversity and complexity of both the static and dynamic processes of forest stratification for these regions can largely be attributed to the wide variations in ways that these forests rely upon release of advance regeneration (Figure 3). This indicates the importance of those kinds of disturbance that serve to release regeneration, such as the various kinds and sizes of windthrows, as compared to disturbances that are lethal to the groundstory such as catastrophic wildfires, landslides, or volcanic eruptions.

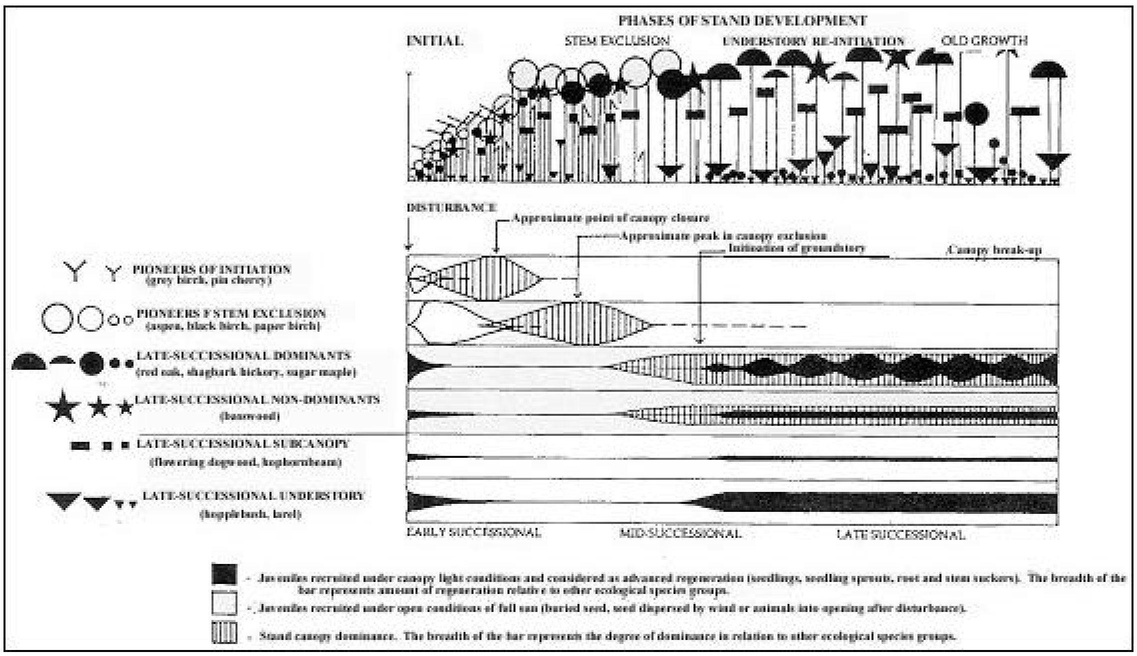

Figure 3. Regeneration recruitment frequency and stand canopy dominance of ecological species groups over different successional stages of stand development for a mixed-hardwood forest of eastern North America. Examples of species are given for each ecological group along with codes denoting their structural position within the stand over time. Note the periodicity recruitment of seedlings for tree species belonging to the late-successi onal canopy dominants (modified after Ashton 1992).

Reliance on release type disturbances in moist forest regions means all growing space is actually occupied before, or shortly after, a disturbance occurs. The term for this type of regeneration initiation has been called allogenic succession, and is often associated with an initial floristics pathway of development (Egler 1954; Drury & Nisbet 1973; Henry & Swan 1974). Disturbance regimes lethal enough to destroy the groundstory can be considered relatively unusual in these forests, but do occur, in many instances associated with human forest clearance for agriculture, mining, and development. Such disturbance patterns often lead to successional processes that promote changes in regeneration dominance characterized by sequential recruitment of different species over time, often in pulses as one species modifies the groundstory environment and facilitates the regeneration of another species. Many examples of this kind of successional process existed during the period of agricultural abandonment in eastern North America in the form of old-field pine and cedar (Lutz 1928; Billings 1938; Oosting 1942; Bormann 1953; Raup 1966). This kind of sequential regeneration initiation has been termed autogenic succession or relay floristics (Clements 1916; Daubenmire 1952; MacArthur & Connell 1966).

Lastly, site specialization of tree species across below-ground resource gradients that are usually related to variations in topography of the landscape can play an important determining role in the spatial heterogeneity of tree mixtures. In general site specialization is more characteristic of late- successional species that are dependent upon advance regeneration as compared to pioneers. Evidence suggests differences in species composition can exist due to edaphic factors: soil moisture (Bourdeau 1954; Ashton et al. 1995; Ashton & Larson 1996) nutrient status (Denslow et al. 1987; Latham 1992; Burslem et al. 1995; Gunatilleke et al. 1996; Gunatilleke et al. in press); biotic factors including density dependence of host-specific seed predation (Janzen 197 1; Condit et al. 1992; 1994), pathogen mortality (Gilbert et al. 1994), seedling herbivory (Becker et al. 1985), and microfaunal and floral symbioses (Janos 1988; Newberry et al. 1988).

RATIONALE FOR DEVELOPMENT OF MIXED-SPECIES PLANTATIONS

Currently moist mixed-species forests supply much of the world demand for quality timber (furniture, interior panelling, flooring, turnery, veneer, and other speciality woods). In most instances the mode of exploitation has led to a high-graded forest that has no quality timber production capability or value. The majority of species that are desired for quality timber in these forests are canopy tree species that are late-successional site-specialists relying upon advance regeneration for their establishment and growth. Studies have shown that their real price values have dramatically increased compared with other timber values such as fiber, pulp, and production sawlogs (Burgess 1993; Howard 1995; Verissimo et al. 1995). Use of tree species that produce quality timber in conventional plantation systems has thus far been generally poor (Wormald 1992; Ashton et al. 1993). This can be mainly attributed to: i) their inability to compete with weedy competition under full sun conditions; ii) their tendency to stagnate or produce poor bole form when self-thinning amongst themselves; and iii) their poor survival and establishment on soils for which such specialists are not suited.

Once established, mixtures of compatible tree species have been demonstrated to have higher yields than single-species plantation systems. Studies in North America have shown greater yields for mixed plantations of *Alnus rubra* (red alder) and *Pseudotsuga menziesii* (Douglas-fir) (Binkley & Greene 1983; Binkley 1984); *Robinia pseudoacacia* (black locust), *Elaeagnus umbellata* (autumn olive), and *Juglans nigra* (black walnut) (Paschke et al. 1989; Schlesinger & Williams 1984); *Quercus rubra* (red oak) and *Tsuga canadensis* (eastern hemlock) (Kelty 1986). European literature has reported similar findings for mixtures of *Betula pendula* (silver birch) and *Pinus sylvestris* (Scots pine) or *Picea abies* (Norway spruce) (Mielikainen 1985; Tham 1988). Only a few well documented studies have been done in the tropics; notable are those by DeBell et al. (1985; 1989) using different mixtures of *Eucalyptus saligna*, *Albizia falcataria* and *Acacia melanoxylon*.

Non-timber species are often associated with the same problems in establishment that characterize late-successional canopy trees. They are also solely exploited from these same forests and are quickly depleted. Many of these species are subcanopy trees, lianas, and groundstory shade-demanding herbs that yield a great variety of specialized but highly desirable products (sugars, latex, spices, medicines, and fruits).

However, these products are usually ecologically costly for the plant to manufacture, and are often associated with chemical compounds that the plant synthesizes for protection. In certain circumstances the management for these products alone can generate more income and produce an higher net present value for a natural forest than any other use for the land (Peters et al. 1989; Balick & Mendelsohn 1992). Examples of single products that continue to rise dramatically in value are *Calamus* spp. (rattan) and *Taxus* spp. (yew), both of which are now multi-billion dollar industries (Manokaran & Wong 1985).

The more reliable and more frequent the yield of a crop plant, the less financial risk, and hence the more desirable for cultivation by landholders. Important examples of such crops are obviously those that are widely grown as intensive single-species plantation systems such as *Camelia sinensis* (tea) or *Hevea brasiliensis* (rubber). Products that produce at infrequent intervals or that take several years to maturity for a one-time harvest are often those plants that are still exploited from natural forests and are most prone to scarcity (Fortmann 1985; DeBeer & McDermott 1989).

We propose that the cultivation of non-timber and quality timber species in mixture, provided the complexities of their autecology are known, can make good economic sense. Mixtures can reduce the downside financial risks of crop failure, and potentially provide a crop yield at least once a year for some species (sugars, latex, fruits). At the same time, mixtures can provide for high value through the sequential yield of several one-time crops that mature over the long-term stand development process. The aggregation of multiple products over time is frequently considerably higher ill net present value than if each species could be grown alone (Peters et al. 1989).

Lastly, in many instances commercial species that are currently grown in single-species plantation systems can also be incorporated into mixed plantation systems, particularly for reduction of crop failure risk from certain pathogens and insects. Under such circumstances these crops can provide a reliable, early and directly marketable product for income during the early stages of plantation establishment. Certain species have often been planted in mixture with a more commercial plant, to provide shade and to avoid sun scorch (*Milicia excelsa* - Gibson & Jones 1977); to reduce leader weevil damage on *Pinus strobus* (eastern white pine) (Boyce 1954) and *Hypsipyla* spp. stem borer damage to host genera of the *Meliaceae* (Africa -*Khaya*, *Entandrophragma*; Asia - *Toona*, *Chukrasia*; S. America - *Swietenia*, *Cedrella*).

A MODEL FOR THE DEVELOPMENT OF MIXED-SPECIES PLANTATIONS

Many studies have recorded the establishment and survival of mixed-species plantations (Worwald 1992). Mixtures have been organized in different ways. Mixtures vary in degree of composition dominance, their spatial arrangement and their age structure. Mixtures of plantings often imply intimate, tree by tree, or line by line establishment, but arrangement can be in blocks such as some of the first mixed planting trials in North America (Hawley & Lutz

1943) and conifer-hardwood mixtures in the United Kingdom (Evans 1984). Mixtures need not always be the result of actual planting. Many studies have now measured the recruitment of natural regeneration beneath the canopy of single-species plantations (Guariguata et al. 1995; Parrotta 1995).

The model that we propose is based largely on knowledge gained of moist mixed-species forest dynamics described in the introduction to this paper. It can be condensed into a list of key principles derived from this understanding:

1. Where soil resources have not degraded or diminished beyond a threshold that affects the ability of more site-specific tree species to establish, or where the radiation environment does not exceed the light tolerance of certain tree species, then plantation establishment of species can be completed at approximately the same time (initial floristics). In situations where site-specific species cannot establish on a plantation site because conditions for their establishment are too severe, then plantation establishment should be sequential over time (relay floristics).

2. To obtain satisfactory growth without continuous thinning it is important to select species that are successionally compatible with each other (Table 1).

Table 1. Examples of successionally compatible mixtures based on some stand development studies in moist forest regions of North America.

	Successional stages of plantation development		
REGION	NURSE PHASE	TRAINING PHASE	TREE CROP PHASE
Southern New England[1]		*Acer rubrum* *Betula lenta*	*Quercus rubra*
Piedmont[2]		*Liriodendron tulipifera*	*Quercus alba*
New Hampshire[3]	*Prunus pensylvanica*	*Betula alleghaniesis*	*Acer saccharum* *Fagus grandifolia*
Northern Michigan[4]		*Populus grandidentata*	*Quercus rubra* *Acer rubrum*
Coastal Washington[5]	*Alnus rubra*	*Pseudotsuga menziesii*	*Tsuga heterophylla*

[1]Oliver 1978; [2]O'Hara 1986; [3]Bormann & Likens 1979; [4]Palk & Pregitzer 1993; [5]Stubblefield & Oliver 1978.

3. The spatial arrangement of mixtures should be consistent with the differential degree of

self-thinning that occurs between tree species that are of different successional status (Table 2). There should be more early-successional species per unit area than late-successional at time of planting. For example this means that in a temperate mixed-species plantation that includes mid-successional *Q. rubra* (red oak) and and early-successional *B. papyrifera* (paper birch) there should be a higher number of B. papyrifera planted than *Q. rubra.*

Table 2. Differences in self thinning over a ten year period (1986-1996) for northern hardwood stands on thin till (xeric) and swale till (mesic) sites at the Great Mountain forest in northeastern Connecticut. Both stands are now 27 years old and would be considered within the stem exclusion stage of stand development (unpublished data from Liptzin & Ashton).

SPECIES	TOLERANCE RANK	% STEM MORTALITY		MORTALITY OF STEMS/ha	
		Till	Swale	Till	Swale
Betula populifolia	very intolerant	-65.4	-100.0	-345	-198
Prunus pensylvanica	very intolerant	-50.0	-46.2	-223	-170
Betula papyrifera	intolerant	-49.1	-47.6	-1704	-694
Betula lenta	intermediate	-40.0	-10.1	-872	-127
Quercus rubra	intermediate	-25.9	-57.9	-609	-992
Fagus grandifolia	tolerant	-13.0	+42.4	-183	+198
Acer rubra	tolerant	-5.9	-6.7	-20	-14
Tsuga canadensis	very tolerant	0.0	0.0	0.0	0.0

4. The spatial arrangement of trees should be compatible with their crown spatial requirements as they grow (Figure 4).

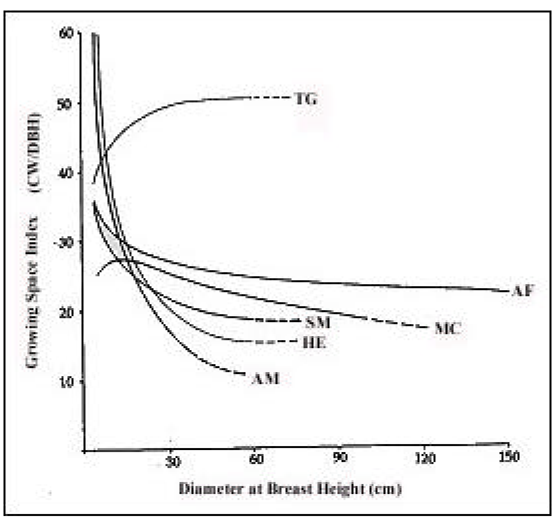

Figure 4. Relationships depicting changes in use efficiency of growing space as measured by the ratio of crown width/ diameter at breast height with increase in diameter at breast height for some tropical tree species of different successional status. [TG - Tectona grandis (mid-successional); AF - Albizia falcataria (mid-successional); MC - Michelia champaca (late-successional); SM - Sweitenia macrophylla (mid-successional); HE - Hibiscus elatus (early-successional); AM - Alstonia macrophylla (early-successional). (Samarasingha et al. 1995).

5. Careful selection of the late- successional more shade tolerant tree species needs to be made to insure their site compatibility.

Our proposed model consists of three phases (Ashton et al. 1993) (Figure 5). These phases of plantation growth represent the same phases described for the natural forest dynamic. The nurse phase can be equated to stand regeneration and initiation; the training phase is the period described as stem exclusion; and the tree crop phase is analogous to the understory initiation and old-growth phase of stand development. All species can be planted simultaneously at establishment, but each species that is selected for the plantation mixture is representative of a different part of the plantation's successional development.

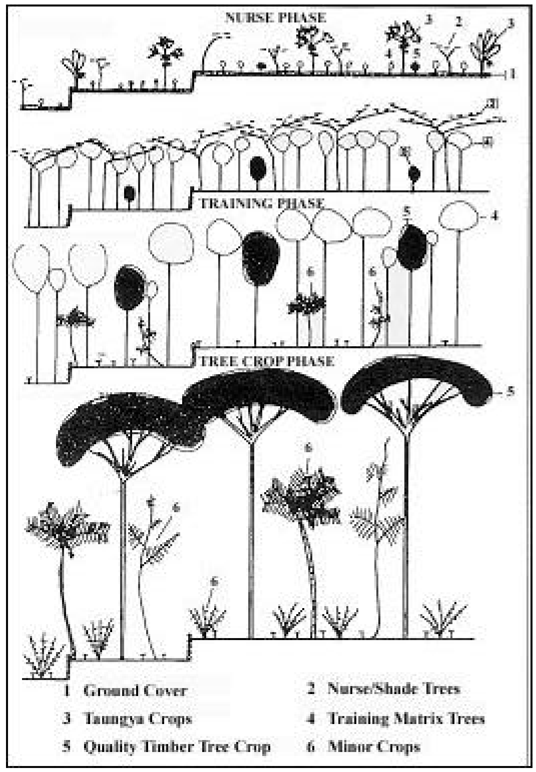

Figure 5. A representation of the progressive development of a mixed-species plantation showing the different phases of development (Ashton et al., 1993).

The Nurse Phase

This period can be considered the most critical time of plantation establishment. Where soil conditions merit restoration and then protection of structure and nutrition, the introduction of pioneer nurse tree and herbaceous species can be used to advantage. Many leguminous ground covers can be selected to imitate the invasive but protective roles that have been recorded for certain early seral herbaceous forbs and grasses (Safford & Filip 1974; Bormarm & Likens 1979). Leguminous ground covers have the added advantage of a low uniform growth habit that can form a compact live mulch. This cover greatly lowers soil surface temperatures, retards soil surface moisture losses from direct evaporation, enriches top soil nitrogen through fixation, and builds soil structure and water holding capacity through increased contributions of organic matter to the soil. All these attributes promote a soil surface cover that is not in direct physical competition for above-ground growing space with the planted tree seedlings.

In certain tropical circumstances where late-successional shade-tolerant tree species are very sensitive to high radiation, early seral pioneer tree species can be established to serve as a shade umbrella. In these regions many pioneers have the rapid growth and crown morphology to create this shade environment. Nurse trees can be seeded or planted at a wide spacing to provide as cheaply and as rapidly as biologically possible a shade environment for the slower growing, more shade-tolerant or -demanding trees species planted beneath. Within two years, nurse pioneer trees can develop a spreading but thin mono-layered crown approximately 4-5 meters above the ground surface. Examples of such species are in the genera *Cecropia, Gliricidia, Macaranga, Mussanga, Rhus and Trema*. Most of these nurse species are very short-lived and die as soon as they are over-topped (Whitmore 1984). Some studies have suggested they may act as temporary nutrient sinks, trapping mineral ions that would otherwise leach out of the soil after a disturbance. As the nurse trees die back they have been suggested to slowly relinquish nutrients back into the soil, making them more available to the other trees (Budowski 1961; Stark 1970; Marks 1974).

Leaves of nurse tree species often have fewer toxic compounds or protective characteristics such as surface wax, hairs or coriaceousness than slower growing tree species (Ewel 1980). Many of these species also have the capability to coppice or pollard and can have high nitrogen contents because they are able to fix atmospheric nitrogen. All these attributes make them suited to producing arboreal fodder for livestock.

During this period of plantation establishment, other very short-lived species can be inter-planted to bring direct tangible benefits to the local community, as long as this does not interfere with future stand dynamics. A successful example of this type of planting for food crops is the taungya system used to establish teak timber plantations in south Asia (Brandis 1897; Champion & Seth 1968). Use of this system encourages protection and care of the tree species that otherwise could be neglected or under-appreciated by the local community. Examples of species that are often socially desirable for local communities include light-demanding high carbohydrate food/fruit crops (*Musa* spp., *Maniot esculenta*, *Carica papaya*). If grown as a commercial crop, the income generated can offset some or all of the costs of plantation establishment.

The Training Phase

When other tree species overtop the shade trees of the nurse phase, fully occupy the plantation canopy, and begin shading out the groundstory cover and crop plants, then the plantation can be considered to have entered the training phase of its development. Tree species that dominate the canopy at this stage typically have autecological characteristics that make them upwardly fast-growing with strong epinastic control. Their crowns are small but compact making them efficient users of growing space. In their native forests they often grow in dense stands and in most circumstances readily self-thin amongst each other. Examples of species that fit this description include many from the genera *Alstonia*, *Betula* (birches), *Eucalyptus* (eucalypts), *Pinus* (pines), and *Populus* (poplars). Many species in these genera are planted as single-species plantations because they can produce some of the world's highest yields of sawtimber and fiber (Evans 1982; Shepherd 1986).

Species characteristic of this group are usually considered pioneers, and produce abundant seed regularly almost every year. Their regeneration is dependent upon seed that germinates on new growing space that has been created by a forest canopy disturbance. Their purpose in the kind of mixed-species plantation that we propose is to provide the same kind of support, stem training and rapid ability to self-thin that improves yield and quality of the slower growing, longer-lived tree species in moist mixed-species forests. If the trees are planted at a dense spacing, thinning regimes can be adjusted to capture their timber and fiber values, or if no markets are available, reliance can be made on their own self-thinning. During the training period of stand development these species create the matrix within which other more shade-tolerant and late-successional species that eventually create the canopy and subcanopy grow. At this time the plantation, like the stem exclusion stage of a moist mixed-species forest, is undergoing considerable self-thinning in the canopy with little to no growing space available to other plants at the groundstory.

On sites with very moderate environmental conditions, or with planted species mixtures that do not require immediate partial shade for survival, the nurse phase of establishment can be very brief. In many moist temperate regions there are no good examples of large-leaved pioneers that germinate and grow. Instead the ground cover is quickly dominated by forbs such as *Rubus* or species in the Compositae, which do not interfere substantially with seedling growth. However, on other sites species such as ferns or members of the Ericaceae may proliferate rapidly, and can interfere with stand development over long time periods. In these circumstances, scarifying the topsoil and then direct seeding pioneer species typically dominant during the training phase along with a temporary ground cover might be a more satisfactory protocol.

Studies have documented the invasive role of many pioneer tree species on abandoned agricultural lands. These are also the species that usually dominate the stand canopy of the training phase of our model. In moist temperate circumstances of eastern North America many species of pines have facilitated the understory initiation of late-successional angiosperms (Lutz 1928; Billings 1938; Oosting 1942; Bormann 1953). Plantations of species with similar growth rate have been documented to facilitate secondary rain forest vegetation in the moist tropics (Guariguata et al. 1995; Parrotta 1995). On sites that have soils and above-ground radiation environments that are too extreme for the immediate establishment of site-sensitive, late-successional species, then plantations should be established by the sequential introduction over time. Using species like *Pinus* as an establishment matrix, the site can quickly be occupied, shading out the groundstory. Afterwards more site-sensitive late- successional species can be under planted or line planted beneath the thinned canopy (Ashton et al. in press).

Tree Crop Phase

The initiation of the tree crop phase of plantation development begins when the late-successional tree species begin to overtop the fast-growing pioneers that dominate the canopy of the training phase. The late-successional species, because they are more shade-tolerant, are able to grow steadily through the stratum of training phase pioneers. During this process, the late- successional species often change canopy morphology dramatically from a crown structure that is monopodial and columnar in shape, to one that upon receiving full sun becomes broadly branched and expansive. These species often do not perform well in competition for growing space with each other, but a more shade- intolerant matrix of pioneers allows for their crown expansion. Although diameter increments might prove low during the training phase, increments should increase substantially as these species attain canopy status during the tree crop phase. These are the species that would be harvested at the end of the rotation for high quality timber products (veneer, furniture, interior paneling, flooring, turnery).

Other species that represent true below-canopy strata of older forests can be grown for the production of various non-timber crops. Because they are adapted to relatively poor light environments many of these species have morphological and physiological adaptations that make them efficient at "harvesting" light. Their leaves are usually broad and often variegated and arranged in single-layers that are either i) in planar whorls that make crowns deep and monopodial; or ii) shallow crowns that are flat and spreading. Their conservative use of resources promotes greater allocation to production of secondary compounds for their protection from pathogens and herbivores. These attributes make them desirable for use as flavorful beverages (obvious commercial examples are the original tea and coffee plants), and medicines. The rotation lengths of these plantations are dependent upon the size and maturity of the canopy late- successional timber trees. The progress of sequentially moving through these phases of plantation development from start to finish could be anywhere between 40 to 100 years depending on the successional dynamic of the mixture chosen for planting and the integrated economic value of the products obtained. Because the subcanopy species, like the late-successional timber species, are slow-growing and site-specific, no satisfactory plantation has been developed to date. However, this aspect of the model deserves testing.

CONCLUSIONS

The growth and development of mixed-species plantations can be understood and managed using an analogue to the development of natural mixed-species stands. Each of the three phases of development corresponds to one the stand development stages of Oliver and Larson (1990): the nurse phase to the stand initiation stage, the training phase to the stem exclusion stage, and the tree crop phase to the understory re-initiation and old-growth stage. Ecologically, each stage is dominated by a different mix of life forms and successional species, while facilitating the regeneration, growth, and development of late-successional or site-sensitive species. Economically, each stage is dominated by a different mix of product yields, offering the possibility of frequent and dependable income compatible with the long-term production of high quality timber. These features suggest mixed-species plantations can offer a variety of social benefits and considerable silvicultural flexibility, while reducing elements of risk often associated with single-species systems.

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