

SURVIVAL AND GROWTH OF *NAUCLEA DIDERRICHII* AND *PERICOPSIS ELATA* IN MONOCULTURE AND MIXED-SPECIES PLOTS IN GHANA

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ADDO-DANSO SD, BOSU PP, NKRUMAH EE, PELZ DR, COKE SA & ADU-BREDU S. 2012. Survival and growth of *Nauclea diderrichii* and *Pericopsis elata* in monoculture and mixed-species plots in Ghana. *Nauclea diderrichii* and *Pericopsis elata* are valuable timber species which are attacked by *Orygmophora mediofoveata* and *Lamprosema lateritialis* respectively in plantations. This study was carried out to evaluate the effects of mixed-species planting on survival and growth of these species. The two species (*N. diderrichii* and *P. elata*) and three other species (*Albizia adianthifolia*, *Terminalia superba* and *Tetrapleura tetraptera*) were planted in various mixtures. Their survival and growth were monitored for 60 months. Generally, survival and growth performance of *P. elata* and *N. diderrichii* were not affected by planting schemes. Trees of both species grew as well in monocultures as they did in mixed stands. Block effect had impact on survival of *P. elata* and height growth of *N. diderrichii*. This indicated the importance of local site variability on survival and growth of the two species. While no significant differences in survival and growth were recorded between monoculture and mixed stands of the two timber species, the socio-economic and ecological advantages of mixtures provide sufficient justification to encourage mixed-species plantations.

Keywords: *Albizia adianthifolia*, *Tetrapleura tetraptera*, *Terminalia superba*, *Orygmophora mediofoveata*, *Lamprosema lateritialis*, herbivory, facilitation, local site variability

ADDO-DANSO SD, BOSU PP, NKRUMAH EE, PELZ DR, COKE SA & ADU-BREDU S. 2012. Kemandirian dan pertumbuhan *Nauclea diderrichii* dan *Pericopsis elata* di plot monokultur dan spesies campur di Ghana. *Nauclea diderrichii* dan *Pericopsis elata* merupakan spesies kayu berharga yang masing-masing diserang oleh *Orygmophora mediofoveata* dan *Lamprosema lateritialis* di ladang. Kajian ini bertujuan untuk menilai kesan penanaman spesies campur terhadap kemandirian dan pertumbuhan kedua-dua spesies pokok. Kedua-dua spesies (*N. diderrichii* dan *P. elata*) dan tiga spesies lain (*Albizia adianthifolia*, *Terminalia superba* dan *Tetrapleura tetraptera*) ditanam dalam kombinasi berbeza. Kemandirian dan pertumbuhan pokok dipantau selama 60 bulan. Umumnya, kemandirian dan pertumbuhan *P. elata* dan *N. diderrichii* tidak dipengaruhi oleh skema penanaman. Kedua-dua spesies tumbuh dengan baik sama ada ditanam secara monokultur atau spesies campur. Blok mempengaruhi kemandirian *P. elata* dan ketinggian *N. diderrichii*. Ini menandakan yang tapak mempengaruhi kemandirian dan pertumbuhan kedua-dua spesies. Walaupun kemandirian dan pertumbuhan ladang monokultur tidak berbeza daripada ladang spesies campur, ladang campuran adalah digalakkan disebabkan kelebihan sosio-ekonomi dan ekologi.

INTRODUCTION

Forests play critical roles in maintaining and providing important ecosystem services (Hector & Bagchi 2007) and functions (Nadrowski et al. 2010). However, these important roles are under threat due to the combined effects of deforestation, forest fragmentation and degradation (Lamb et al. 2005, FAO 2010). Concerns about these threats have mainly focused

on their impacts on habitat quality, climate change and particularly biological diversity (Shukla et al. 1990, Benhin & Barbier 2004, Amisah et al. 2009). Tree diversity of forested ecosystems has important consequences on carbon storage, decomposition or mineral cycling, nutrient acquisition, communities of biota, and growth and productivity (Forrester et al. 2005, Piotta

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2008, Nadrowski et al. 2010, Zeugin et al. 2010). Species such as *Nauclea diderrichii* (opepe) and *Pericopsis elata* (afroformosa) are among the most economically important hardwood species in tropical Africa, particularly Ghana (Fonweban et al. 1994, Oteng-Amoako 2006, Foli et al. 2009). These species are important for decorative and structural purposes and have high resistance to fungal decay (Oteng-Amoako 2006, Orwa et al. 2009). Apart from timber, both species are also known to provide other products and services. *Pericopsis elata*, for instance, is an important shade tree in the cocoa growing areas of Ghana (Anglaare 2005). *Nauclea diderrichii* is used in preparing soups and also serves as a source of fodder for livestock (Orwa et al. 2009). Furthermore, the leaves and bark of *N. diderrichii* are used in treating several ailments in most rural communities in Ghana (Addo-Fordjour et al. 2008).

However, overexploitation coupled with paucity in natural regeneration threatens the long-term existence of these species (Oteng-Amoako 2006). Attempts to grow *N. diderrichii* and *P. elata* in plantations have generally been hampered by attacks from *Orygmophora mediofoveata* (Lepidoptera: Noctuidae) and *Lamprosema lateritialis* (Lepidoptera: Pyralidae) respectively (Wagner et al. 2008). Studies have shown that these specialist insect herbivores can cause serious damage to especially young plantations of *N. diderrichii* and *P. elata* (Atuahene 1996, Bosu et al. 2004). Caterpillars of *O. mediofoveata* infest terminal shoots by boring into the nodes especially the apical shoots and heavy multiple attacks usually lead to death. The pyralid moth, *L. lateritialis* is restricted to West and Central Africa but widespread in lowland rainforests of Ghana, Nigeria and Cote d'Ivoire (Wagner et al. 2008). This defoliator feeds gregariously on leaves of *P. elata* leading to reduced growth and eventually death when defoliation is very persistent (Atuahene 1996). Unfortunately, no studies have been done to assess alternative management strategies for these economically important insect herbivores. One silvicultural approach which is gaining much attention in recent times is the use of tree species mixtures to enhance stand diversity (Jactel & Brockerhoff 2007). Although there is no consensus on the effects of mixed stands on insect pests (Bosu et al. 2006, Vehviläinen et al.

2007, Schuldt et al. 2010, Plath et al. 2011a), and growth and productivity (Wormald 1992, Piotto 2008, Nadrowski et al. 2010), one advantage is that planting these high risk species in a matrix of non-host tree species can reduce risk of pest attack and damage, thereby increasing productivity and growth (Montagnini et al. 1995, Kelty 2006).

The objectives of this study were to (1) evaluate the effects of different planting schemes on survival of *N. diderrichii* and *P. elata* and (2) determine whether *N. diderrichii* and *P. elata* grew better in monocultures or in mixture with other species. The hypothesis was that plots with lower densities of *N. diderrichii* and *P. elata* would have reduced damage leading to lower seedling mortality and higher growth rates.

MATERIALS AND METHODS

Site description

The 1 ha experimental plantation was established in June 2005 on a heavily degraded site in the Bia Tano Forest Reserve located in the Goaso Forest District, Ghana. The site, located in the moist semi-deciduous forest zone (Hall & Swaine 1981), is dominated by soils which are weathered with low activity kaolinitic clays but quite productive (Owusu-Bennoah et al. 2000). The plot lies between 07° 58.5' N and 02° 01.3' W with mean altitude of 20.3 m above sea level (asl). Annual precipitation ranges between 1500 and 1700 mm per year and there is a long dry season between December and March, with a short dry season in August and September. Mean monthly minimum and maximum temperatures vary between 26 and 29 °C. The area which was dominated by grass was cleared manually and adequately prepared for planting.

Planting schemes and experimental design

Seedlings of *N. diderrichii*, *P. elata*, *Albizia adianthifolia*, *Tetrapleura tetraptera* and *Terminalia superba* were raised in polythene bags and planted at an average height of 30 cm. Apart from *P. elata*, which is a non-pioneer light demander (Agyeman et al. 1999), all the other species are pioneers (Oteng-Amoako 2006). Seedlings from *A. adianthifolia* were raised from seeds collected from a source in the dry semi-deciduous

forest zone, while seeds for the other species were collected from sites within the moist semi-deciduous forest zone. Species selection for the plantation was based on conservation concerns (Benhin & Barbier 2004, Oteng-Amoako 2006), relevance for plantation development in Ghana, potential economic values and provision of non-wood goods and services (Diabete et al. 2005, Swaine et al. 2005, Foli et al. 2009). The plantation consists of 20 contiguous 10 × 10 m plots with one, two or four tree species per plot. Seedlings of focal species, *N. diderrichii* and *P. elata* were planted in (1) monoculture (100% *Nauclea* or 100% *Pericopsis*), (2) two-species mixtures (50% *Nauclea*, 50% *Albizia* or 50% *Pericopsis*, 50% *Albizia*) and (3) four-species mixture (25% *Nauclea*, 25% *Pericopsis*, 25% *Terminalia*, 25% *Tetrapleura*) at the same time. There were a total of 36 trees per plot and planting distance was 2 m between trees. A distance of 3 m was left between plots to avoid possible edge effects. The layout of the experiment was randomised block design, with four replicates for each planting scheme. The blocks were laid horizontally along the contours of the gentle sloping landscape. Block 1 was placed at the highest contour, followed by the other blocks. Block 4 was in the lowest contour and closest to a nearby stream. Seedlings in four-species mixture plots were randomly distributed, while seedlings in monoculture and two-species mixture plots were planted in rows.

In two-species mixture plots, rows planted with *Nauclea* or *Pericopsis* alternated with rows containing *Albizia*. Plots were maintained by regularly clearing *Chromolaena odorata* and other competing vegetation. No other silvicultural manipulations were carried out.

Measurements and data analyses

Initial measurements for survival and growth patterns were taken 6 months after planting, and subsequently at one-year intervals. However, assessments could not be carried out in 2006 and 2009 due to logistical constraints. Survival of focal species was determined by counting the number of individual plants in each plot. The total number of plants per species was calculated and subsequently the survival (%) of *N. diderrichii* and *P. elata* in monoculture and mixed plots was determined. Survival was compared for the two

species and the different planting schemes of each focal species using χ^2 test. Growth assessments of focal species in different planting schemes were done by measuring either the diameter at 10 cm from the soil level or at 130 cm breast height (dbh) when the trees had grown above 140 cm and total height. Relative growth rates (RGRs) for height and diameter of *N. diderrichii* and *P. elata* were calculated using the formula from Adu-Bredu and Hagihara (2003):

$$\text{RGR} = \frac{1}{w} \times \frac{\Delta w}{\Delta t} = \frac{\ln w_2 - \ln w_1}{t_2 \pm t_1}$$

where Δw and Δt were changes in tree dimensions (diameter or height) and time respectively, w_1 and w_2 were tree dimensions (diameter or height) at the beginning and end of the period while t_1 and t_2 , the corresponding assessment period in months. Growth was assessed by two-way analysis of variance (ANOVA), with planting scheme and block as fixed factors at $\alpha = 5\%$ level of significance.

For multiple comparisons in ANOVA analysis, LSD post-hoc tests were applied. Prior to analysis, data were transformed where necessary to comply with assumptions of normality and variance homogeneity for parametric tests. Growth assessment (diameter and height) values were log-transformed before analysis. All statistical analyses were conducted using Microsoft Office Excel 2003 computer spreadsheet software.

RESULTS

Survival of *Nauclea diderrichii* and *Pericopsis elata*

There was no significant difference in survival between *N. diderrichii* and *P. elata* ($\chi^2 = 0.44$, $df = 1$, $p = 0.979$), and the different planting schemes of the two species (*N. diderrichii*: $\chi^2 = 0.51$, $df = 2$, $p = 0.756$; *P. elata*: $\chi^2 = 0.28$, $df = 2$, $p = 0.866$) (Figure 1). Mortality was recorded in both species but was relatively high in *N. diderrichii* at 60 months. In *P. elata*, 150 individual trees survived after 10 months (59.5%, $n = 252$), out of which monoculture plots contributed 87 individuals ($n = 144$). There was, however, considerable decline in survival of *N. diderrichii* (35.3%, $n = 252$) during the first 60 months after plantation establishment (Figure 1). During the same

period, survival for *N. diderrichii* was 35.4% in monoculture plots, 37.5 and 30.6% in two-species (50% *Nauclea*) and four-species (25% *Nauclea*) mixture plots respectively (Figure 1). Survival of *N. diderrichii* was significantly affected by planting scheme at 6 months of establishment ($\chi^2 = 15.05$, $df = 2$, $p = 0.005$). Survival for *N. diderrichii* at this age was 70.8, 63 and 38.9% in monoculture, two- and four-species mixtures respectively (Figure 1). There was highly significant block effect (results not shown) on survival of *P. elata* after 60 months ($\chi^2 = 31.439$, $df = 3$, $p = 0.004$).

During this period, the highest survival in *P. elata* was recorded in block 2 (76.2%), while blocks 3 and 1 recorded 65.1 and 61.9% respectively (results not shown). Block 4 recorded the least survival of 34.9% (results not shown).

Growth patterns of *Nauclea diderrichii* and *Pericopsis elata*

Height and diameter

After 60 months of plantation establishment, *N. diderrichii* grew taller ($6.8 \text{ m} \pm 0.17$) on average in all planting schemes than *P. elata* ($3.1 \text{ m} \pm 0.11$) (Figure 2). *Nauclea diderrichii* also had greater mean diameter ($9.5 \text{ cm} \pm 0.33$) than *P. elata* ($3.9 \text{ cm} \pm 0.06$) at 60 months (Figure 3). There was no significant difference in height and diameter between monoculture and mixed stands of the two species. At this age, individual *N. diderrichii* trees, however, attained greater diameter and height in 50% mixture than monoculture and 25% mixture stands (Figures 2 and 3). Mean diameter for individual *P. elata*

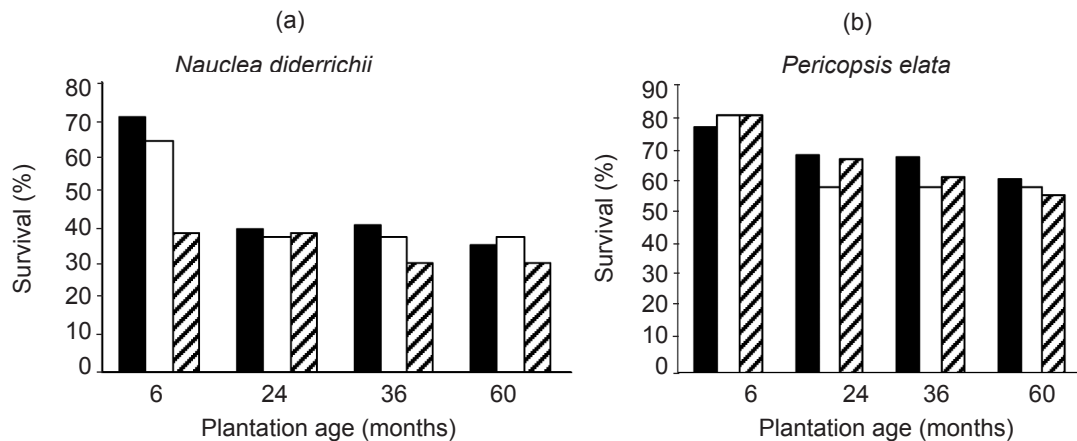


Figure 1 Survival of focal species (a) *Nauclea diderrichii* and (b) *Pericopsis elata* at different stand ages. Seedlings were grown in different planting schemes: monocultures (dark bars), 50% mixture (open bars) and 25% mixture (diagonal bars)

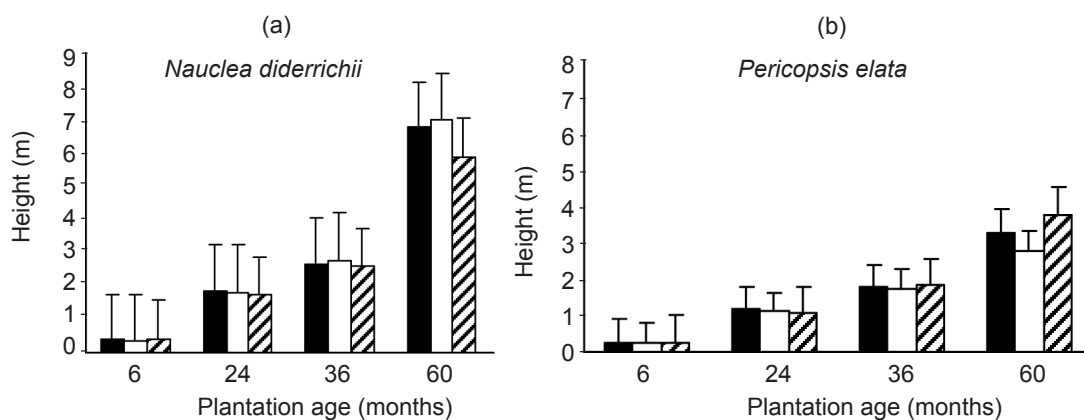


Figure 2 Tree height (mean \pm SE) for (a) *Nauclea diderrichii* and (b) *Pericopsis elata* at different stand ages. Seedlings were grown in different planting schemes: monocultures (dark bars), 50% mixture (open bars) and 25% mixture (diagonal bars)

trees was slightly higher in monocultures than mixed plots. On the contrary, mean height for *P. elata* was high in 25% mixture stands compared with monocultures and 50% mixture stands (Figure 2). Height of *N. diderrichii* was not significantly affected by different planting schemes ($F = 5.431$, $df = 2$, $p = 0.05$) after 6 months of establishment. *Nauclea diderrichii* seedlings in monoculture plots recorded a mean height of $0.43 \text{ m} \pm 0.027$, while seedlings in 50 and 25% mixtures recorded mean heights of $0.36 \text{ m} \pm 0.030$ and $0.44 \text{ m} \pm 0.006$ respectively. At the same period, block had significant effect on height of *N. diderrichii* ($F = 6.034$, $df = 3$, $p = 0.030$). Seedlings of *N. diderrichii* in monocultures and mixed stands grew taller on average in block 2 ($0.49 \text{ m} \pm 0.031$), followed by block 3 ($0.40 \text{ m} \pm 0.035$), block 1 ($0.36 \text{ m} \pm 0.035$) and block 4 ($0.26 \text{ m} \pm 0.025$) (results not shown). However, height growth was significantly

different between blocks 2 and 4 as well as blocks 3 and 4 (results not shown).

Relative growth rate

Mean RGR in height (RHGR) for *N. diderrichii* was high in monocultures ($1.95 \pm 0.036 \text{ m m}^{-1} \text{ month}^{-1}$), followed by 50% ($1.87 \pm 0.143 \text{ m m}^{-1} \text{ month}^{-1}$) and 25% mixtures ($1.66 \pm 0.166 \text{ m m}^{-1} \text{ month}^{-1}$) (Table 1). Mean RGR in diameter (RDGR) for *N. diderrichii* was, however, relatively high in 25% mixture ($2.29 \pm 0.151 \text{ cm cm}^{-1} \text{ month}^{-1}$) but lowest in 50% mixture ($2.16 \pm 0.038 \text{ cm cm}^{-1} \text{ month}^{-1}$). Mean RHGR and RDGR for *P. elata* were also high in monocultures (Table 1). Mean RDGR for *P. elata* in mixed stands was higher in 50% mixture ($1.37 \pm 0.182 \text{ cm cm}^{-1} \text{ month}^{-1}$) than 25% mixture ($1.27 \pm 0.074 \text{ cm cm}^{-1} \text{ month}^{-1}$) (Table 1). There was no significant difference between planting schemes of the two species.

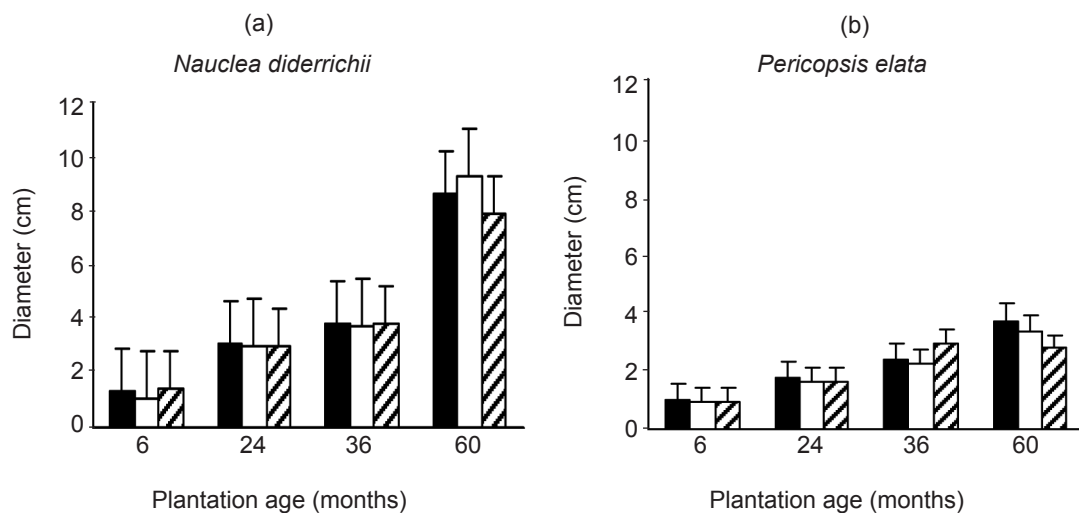


Figure 3 Tree diameter (mean \pm SE) for (a) *Nauclea diderrichii* and (a) *Pericopsis elata* at different stand ages. Seedlings were grown in different planting schemes: monocultures (dark bars), 50% mixture (open bars) and 25% mixture (diagonal bars).

Table 1 Relative growth rates (mean \pm SE) in height (RHGR) and diameter (RDGR) for *Nauclea diderrichii* and *Pericopsis elata* in different planting schemes

Planting scheme	<i>Nauclea diderrichii</i>		<i>Pericopsis elata</i>	
	RHGR ($\text{m m}^{-1} \text{ month}^{-1}$)	RDGR ($\text{cm cm}^{-1} \text{ month}^{-1}$)	RHGR ($\text{m m}^{-1} \text{ month}^{-1}$)	RDGR ($\text{cm cm}^{-1} \text{ month}^{-1}$)
Monoculture	$1.95(\pm 0.036)$	$2.25(\pm 0.038)$	$1.19(\pm 0.055)$	$1.39(\pm 0.053)$
50% mixture	$1.87(\pm 0.143)$	$2.16(\pm 0.170)$	$1.02(\pm 0.066)$	$1.37(\pm 0.182)$
25% mixture	$1.66(\pm 0.166)$	$2.29(\pm 0.151)$	$1.09(\pm 0.075)$	$1.27(\pm 0.074)$

DISCUSSION

Survival of *Nauclea diderrichii* and *Pericopsis elata*

Even though there was no significant difference, survival varied between *N. diderrichii* and *P. elata* after 60 months of plantation establishment, indicating that species-specific traits were influenced by environmental conditions (Potvin & Gotelli 2008, Plath et al. 2011a). Mortality was relatively low in *P. elata* compared with *N. diderrichii*. Studies in Ghana have shown that the distribution of many forest trees tends to show very strong association with climatic and soil conditions (Hall & Swaine 1981, Swaine 1996). The experimental plantation was established in a site which happened to be the natural ecological range for *P. elata* (Atuahene 1996). *Nauclea diderrichii*, on the contrary, is known to be rare outside its natural range (Onyekwelu et al. 2003). Planting of species in conditions which are different from those of its natural range has the tendency to cause problems (Wormald 1992). Survival in both species was least in the 25% mixture (comprising *N. diderrichii*, *P. elata*, *T. superba* and *T. tetraptera*) compared with other planting schemes at 60 months (Figure 1). All species in that planting scheme required sufficient overhead light to establish (Agyeman et al. 1999, Oteng-Amoako 2006), therefore, competition for light could have intensified.

The deep shade created by particularly *T. superba* (very fast-growing species) could have reduced the quantum of photosynthetic active radiation required by *N. diderrichii* and *P. elata*, causing the seedlings to become etiolated and eventually die (Bosu et al. 2006, Kelty 2006). We also speculated that the survival in either species could have also been partly influenced by attacks from their primary insect pests. Bosu (2005) working in the same experimental plantation observed various stages of dieback and defoliation in *N. diderrichii* and *P. elata* respectively at 6 months of establishment. Due to this, some of the *Nauclea* trees eventually developed multiple stems, a response of the species to apical shoot damage (Leakey 1990, Orwa et al. 2009). At 6 months, there was significant planting scheme effect on survival of *N. diderrichii*, indicating that the different planting regimes had influence on survival of *Nauclea*. Results for survival in *P. elata* at 60 months showed that small-scale

plot variability could have significant impact on success of species grown in plantations (Plath et al. 2011a). At this age, survival in *P. elata* was significantly influenced by block. This result corroborates the findings of a study in Sardinilla, Central Panama (Plath et al. 2011a). Variations in soil properties, topography and drainage within experimental plots can influence survival rates (Healy et al. 2008, Potvin & Gotelli 2008, Plath et al. 2011a). Even though prior to the experiment soil analysis was not carried out for plots containing different diversity levels, field observation showed a possible variability in the soil properties and other microsite conditions. The site had gentle sloping topography and some plots in block 4 were laid at the lowest portion of the slope closest to a stream. A casual look at the data revealed relatively high mortality in plots located in block 4 compared with other blocks.

Growth of *Nauclea diderrichii* and *Pericopsis elata*

Growth performance of *N. diderrichii* and *P. elata* was not significantly different between planting regimes at 60 months of plantation establishment. This implied that individual trees of both species grew as well in monoculture as they did in mixed stands. This result is in line with other studies in Puerto Rico and Panama (Parrotta 1999, Plath et al. 2011a, b). Plath et al. (2011b) working at Sardinilla in Panama found that growth performance of *Tabebuia rosea* and *Cedrela odorata* were not significantly affected by planting regimes within the first 2 years after establishment. The present result showed that the companion species did not play any facilitative or competitive reduction roles in the growth performance of the two focal species (Plath et al. 2011b). Even the presence of nitrogen-fixing species *A. adianthifolia* and *T. tetraptera* did not significantly affect growth performance. Studies in Puerto Rico and Panama have shown that facilitative interactions do not always produce greater growth in mixtures compared with monocultures (Parrotta 1999, Plath et al. 2011b). Parrotta (1999) found that the admixture with either *Casuarina equisetifolia* or *Leucaena leucocephala* after 8.5 years had little or no effect on the growth and productivity of *Eucalyptus robusta*. Plath et al. (2011b) also reported that the presence of *Gliricidia sepium* had no significant influence on the growth of *C. odorata* and *T.*

rosea. According to Binkley and Gardina (1997), net primary production could be greater in mixture if one species could obtain more of a limiting resource. Thus, the presence of the nitrogen-fixing species could neither accelerate rates of photosynthesis nor enhance efficient use of resources such as water and nutrient (Richards et al. 2010). Since facilitation is mostly species-specific, some species may either have positive, negative or neutral effects on others (Callaway 1998, Piotto 2008, Nadrowski et al. 2010). The result showed that 60 months after establishment, individual *Nauclea* trees in 50% mixture had high growth despite that particular planting regime recording least growth from 6 to 36 months (Figures 2 and 3). This indicated that a significant facilitative effect could develop with time (Plath et al. 2011b) and that rates of nitrogen fixation could increase with age (Richards et al. 2010). Climate, topography and soil nutrient supply are important factors which can alter tree interactions in forest stands (Nichols et al. 2001, Healy et al. 2008). The influence of these factors, therefore, makes it difficult to predict sites that can lead to increased growth and productivity in mixed-species plantations (Forrester et al. 2005). Lack of significant influence of *A. adianthifolia* and *T. tetraptera* on growth of either *N. diderrichii* or *P. elata* may have been partly due to prevailing soil factors (Forrester et al. 2005, Swaine et al. 2005). Wormald (1992) noted that for nitrogen-fixing species to make a positive contribution to stand growth, the site conditions must be suitable.

The amount and rate of nitrogen fixation by nitrogen-fixing species depend very much on soil and any other factor which affect plant growth (Forrester et al. 2007). A study by Swaine et al. (2005) showed that the capacity for *A. adianthifolia* to form nodules was strong when soil nitrogen was in low supply. The same study also reported that the importance of *A. adianthifolia* was greatest in dry forest zones (Swaine et al. 2005). Results at 6 months of establishment showed a significant block effect on *N. diderrichii* height. This result is in line with a study by Nichols et al. (2001) who reported a significant effect of block on height growth of *Terminalia amazonia*, which they attributed to the topography of the site. In another study in Ghana, Baker et al. (2003) found that topographic position had significant effect on the soil water regime at lower positions

in the topography. They also indicated that total C, total N and exchangeable K concentrations significantly declined down slope (Baker et al. 2003).

CONCLUSIONS

Both species, *N. diderrichii* and *P. elata*, performed equally well either in monoculture or mixed-species stands. With hardly any differences in survival and growth rates between the various planting schemes, plantations of both *N. diderrichii* and *P. elata* can be established using a range of species combinations and ratios.

The response of the two focal species to the different planting schemes and variability in local site factors was temporal. Planting both species in their natural ecological range could increase their survival and growth rates. The inclusion of *A. adianthifolia* and *T. tetraptera* could not significantly influence the growth of both species. However, a facilitative effect can develop with time as *A. adianthifolia* helps improve soil conditions through nitrogen fixation. *Tetrapleura tetraptera* in mixed plots started fruiting after about two and a half years following the establishment of the plots. In practice, smallholder tree growers integrating *T. tetraptera* in their tree plantations can derive intermediary benefits by harvesting and selling the fruits to supplement their incomes as they wait for the focal species to mature. It is important to encourage mixed-species plantations to help achieve diverse economic, silvicultural and ecological goals.

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REFERENCES

- ADDO-FORDJOUR P, ANNING AK, BELFORD EJB & AKONNOR D. 2008. Diversity and conservation of medicinal plants in the Bomaa community of the Brong Ahafo region, Ghana. *Journal of Medicinal Plants Research* 2: 226–233.
- ADU-BREDU S & HAGIHARA A. 2003. Long-term carbon budget of the above-ground parts of a young hinoko cypress (*Chamaecyparis obtuse*) stand. *Ecological Research* 18: 165–175.

- AGYEMAN VK, SWAINE MD & THOMPSON J. 1999. Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology* 87: 815–827.
- AMISAH S, GYAMPOH AB, SARFO-MENSAH P & QUAGRAINE KK. 2009. Livelihood trends in response to climate change in forest fringe communities of the Offin basin in Ghana. *Journal of Applied Sciences and Environmental Management* 13: 5–15.
- ANGLAAERE LCN. 2005. Improving the productivity and sustainability of cocoa farms in West Africa through utilization of native forest trees in agroforestry systems. PhD thesis, University of Wales, Bangor.
- ATUAHENE SKN. 1996. Effects of defoliation on *Pericopsis elata* (Harms.) van Meewan by the leaf tying moth, *Lamprosema lateritialis* Hampson (Lepidoptera: Pyralidae). *Ghana Journal of Forestry* 2: 1–5.
- BAKER TR, BURSLEM DFRN & SWAINE MD. 2003. Associations between tree growth, soil fertility and water availability at local and regional scales in Ghana tropical rainforest. *Journal of Tropical Ecology* 19: 109–125.
- BENHIN JKA & BARBIER EB. 2004. Structural adjustment programme, deforestation and biodiversity loss in Ghana. *Environmental and Resource Economics* 27: 337–366.
- BINKLEY D & GARDINA C. 1997. Nitrogen fixation in tropical forest plantations. Pp 297–337 in Nambia EKS & Brown AG (eds) *Management of Soil, Nutrients and Water in Tropical Plantation Forests*. CSIRO/ACIAR, Canberra.
- BOSU PP. 2005. Restoration, conservation, and sustainable production of indigenous timber species in the Goaso District of Ghana. Progress report submitted to TBI-Ghana.
- BOSU PP, ADU-BREDU S & NKURUMAH EE. 2004. Observations of insect pest activities within selected nurseries in Ashanti, Ghana. Pp 154–162 in Cobbinah JR, Ofori DA & Bosu PP (eds) *Pest Management in Tropical Plantations. International Workshop Proceedings*. 21–23 July 2004, Kumasi.
- BOSU PP, COBBINAH JR, NICHOLS JD, NKURUMAH EE & WAGNER MR. 2006. Survival and growth of mixed plantations of *Milicia excelsa* and *Terminalia superba* 9 years after planting in Ghana. *Forest Ecology and Management* 233: 352–357.
- CALLAWAY RM. 1998. Are positive interactions species-specific? *Oikos* 82: 202–207.
- DIABETE M, MUNIVE A, DE FARIA SM, BA A, DREYFUS B & GALIANA A. 2005. Occurrence of nodulation in unexplored leguminous trees native to the West African tropical rainforest and inoculation response of native species useful in reforestation. *New Phytologist* 166: 231–239.
- FAO 2010. *Global Resources Assessment 2010. Country Report, Ghana*. FAO, Rome.
- FOLI E, AGYEMAN VK & PENTSIL M. 2009. *Ensuring Sustainable Timber Supply in Ghana: A Case for Plantations of Indigenous Timber Species*. Technical Note No. 1. Forestry Research Institute of Ghana, Kumasi.
- FONWEBAN JN, DONDJANG JP & CHAPAJONG TN. 1994. Growth and quality responses of bilinga (*Nauclea diderrichii* Merrill.) to spacing. *New Forests* 8: 387–395.
- FORRESTER DI, BAUHUS J & COWIE AL. 2005. On the success and failure of mixed-species plantations: lessons learned from model system of *Eucalyptus globulus* and *Acacia meansii*. *Forest Ecology and Management* 209: 147–155.
- FORRESTER DI, SHORTEMEYER M, STOCK WD, BAUHUS J, KHANNA PK & COWIE AL. 2007. Assessing nitrogen fixation in mixed- and single-species plantations of *Eucalyptus globulus* and *Acacia mearnsii*. *Tree Physiology* 27: 1319–1328.
- HALL JB & SWAINE MD. 1981. *Geobotany-Distribution and Ecology of Vascular Plants in Tropical Rainforest Forest Vegetation in Ghana*. Dr W Junk Publishers, the Hague.
- HEALY C, GOTELLI NJ & POTVIN C. 2008. Partitioning the effects of biodiversity and environmental heterogeneity for productivity and mortality in a tropical tree plantation. *Journal of Ecology* 96: 903–913.
- HECTOR A & BAGCHI R. 2007. Biodiversity and ecosystem multifunctionality. *Nature* 448: 188–190.
- JACTEL H & BROCKERHOFF EG. 2007. Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10: 835–848.
- KELTY M. 2006. The role of species mixtures in plantation forestry. *Forest Ecology and Management* 233: 195–204.
- LAMB D, ERSKINE FD & PARROTTA JA. 2005. Restoration of degraded tropical forest landscapes. *Science* 301: 1628–1632.
- LEAKEY RRB. 1990. *Nauclea diderrichii*: rooting of stem cuttings, clonal variation in shoot dominance and branch plagiotropism. *Trees* 4: 164–169.
- MONTAGNINI F, GONZÁLEZ E & PORRAS C. 1995. Mixed and pure forest plantations in the humid neotropics: comparison of early growth, pest damage and establishment costs. *Commonwealth Forestry Review* 74: 306–314.
- NADROWSKI K, WIRTH C & SCHERER-LORENZEN M. 2010. Is forest diversity driving ecosystem function and services? *Current Opinion in Environmental Sustainability* 2: 75–79.
- NICHOLS JD, ROSEMEYER ME, CARPENTER FL & KETTLER J. 2001. Intercropping legume tree with native timber trees rapidly restores cover to eroded tropical pasture without fertilization. *Forest Ecology and Management* 152: 195–209.
- ONYEKWELU JC, KATEB EL, STIMM HB & MOSANDL R. 2003. Growth characteristics of *Nauclea diderrichii* (De Wild.) in unthinned plantations in south-western Nigeria. Pp 147–163 in Mosandl R, El Kateb H & Stimm B (eds) *Waldbau-weltweit*. Beiträge zur Internationalen Waldbauforschung Forstliche Forschungsberichte, Munich.
- ORWA C, MUTUA A, JAMNADASS R & ANTHONY S. 2009. *Agroforestry Database: A Tree Reference and Selection Guide Version 4.0*. [Http://www.worldagroforestry.org/sites/tree_dbs/treedatabases.asp](http://www.worldagroforestry.org/sites/tree_dbs/treedatabases.asp). Accessed 22 December 2009.
- OTENG-AMOAKO AA. 2006. *100 Tropical African Trees From Ghana. Tree Description and Wood Identification With Notes on Distribution, Ecology, Silviculture, Ethnobotany and Uses*. Graphic Packaging, Accra.
- OWUSU-BENNOAH E, AWADZI TW, BOATENG E, KROGH L, BREUNING-MADSEN H & BORGGAARD OK. 2000. Soil properties of a toposequence in the moist semi-deciduous forest zone of Ghana. *West African Journal of Applied Ecology* 1: 1–10.

- PARROTTA JA. 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: 45–77.
- PIOTTO D. 2008. A meta-analysis comparing tree growth in monocultures and mixed plantation. *Forests Ecology and Management* 225: 781–786.
- PLATH M, MODY K, POTVIN C & DORN S. 2011a. 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: 741–750.
- PLATH M, MODY K, POTVIN C & DORN S. 2011b. Do multipurpose companion trees affect high value timber trees in a silvopastoral plantation system? *Agroforestry Systems* 81: 79–92.
- POTVIN C & GOTELLI NJ. 2008. Biodiversity enhances individual performances but does not affect survivorship in tropical trees. *Ecology Letters* 11: 217–223.
- RICHARDS AE, FORRESTER DI, BAUHUS J & SCHERER-LORENZEN M. 2010. The influence of mixed plantations on the nutrition of individual species. *Tree Physiology* doi 10.1093/treephys/tpq 035.
- SCHULDT A, BARUFFOL M, BÖHNKE M, BRUELHEIDE H, HÄRDITTE W, LANG AC, NADROWSKI K, OHEIMB G, VOIGHT W, ZHOU H & ASSMAN T. 2010. Tree diversification promotes insect herbivory in subtropical forests of South-East China. *Journal of Ecology* 98: 917–926.
- SHULKA J, NOBRE C & SELLERS P. 1990. Amazon deforestation and climate change. *Science* 247: 1322–1325.
- SWAINE MD. 1996. Rainfall and soil fertility as factors limiting forest species distribution in Ghana. *Journal of Ecology* 84: 419–428.
- SWAINE EK, KILLHAM KS & SWAINE MD. 2005. The response of *Albizia adianthifolia* to rhizobium and nitrogen in forest-grown and greenhouse-grown seedlings. *Ghana Journal of Forestry* 17 & 18: 1–8.
- VEHVILÄINEN H, KORICHERA J & RUOHOMÄKI K. 2007. Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term experiments. *Oecologia* 152: 287–298.
- WAGNER MR, COBBINAH JR & BOSU PP. 2008. *Forest Entomology in West Africa: Forest Insects of Ghana*. Second edition. Springer, Dordrecht.
- WORMALD TJ. 1992. *Mixed and Pure Forest Plantations in the Tropics and Subtropics*. FAO Working Paper No. 11291. FAO, Rome.
- ZEUGIN F, POTVIN C, JANS J & SCHERER-LORENZEN M. 2010. Is tree diversity an important driver for phosphorus and nitrogen acquisition of a young tropical plantation? *Forest Ecology and Management* 269: 1424–1435.