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Native forest regeneration in pine and eucalypt plantations in Northern Province, South Africa

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Abstract

Commercial plantations in South Africa have been established mainly in grasslands adjacent to native forest which occur as small, scattered patches, restricted to valleys and scarps by regular fires in the adjacent fire-prone grasslands. Understorey vegetation was sampled in plantation stands of different age of *Pinus patula*, and old stands of *P. elliottii*, *P. taeda* and *Eucalyptus saligna*, growing on the forest margin. The study was done in two areas in Northern Province, South Africa (23°S to 25°S, and 30°E to 31°E): Woodbush-De Hoek along the Eastern Escarpment, and Entabeni on Soutpansberg mountains. The area receives 1200 to 1900 mm rain per annum, mainly during summer. Two hypotheses were tested: understorey colonisation by native plant species is strongly influenced by the overhead plantation species; and abundance and diversity of indigenous woody and herbaceous species increase with increasing stand age. A total of 170 species were recorded on 62 plots of 78.5 m^2 each, and included all major growth forms present in the surrounding forest, except epiphytes. Trees were represented by 62 species, but only 18% of these occurred in more than 10% of the plots. Seventy-two percent of the 95 tree, shrub and climber species are animal-dispersed but only 22% of the animal-dispersed species occur in more than 10% of the plots. Mean clean bole length of the plantation stand gave the best regression coefficients with species richness, stem density, mean DBH and mean height of the woody regeneration, all of which increased with stand age. There was no clear pattern in understorey species composition among the different plantation species. Site factors such as substrate (geology) and temperature (altitude and radiation index) had a strong correlation with species composition and density of understorey vegetation. The results do demonstrate a useful successional process which could be used to achieve specific management objectives at relatively low costs. Potential applications of this succession process are manipulation of tree stands (commercial plantations or invader plants) to restore native forest biodiversity, control of understorey weeds in commercial plantations, and growing of useful crops under tree canopies. © 1997 Elsevier Science B.V.

Keywords: Afforestation; Eucalyptus; Evergreen forest; Pinus; Restoration; Succession

1. Introduction

Uncontrolled timber harvesting and clearing of forests for agriculture in tropical to temperate regions contribute to the loss of biodiversity, decline in valued species and productivity, and raise concern over other direct and indirect benefits of forests. Several studies have indicated that tree plantings of both introduced and native species are associated with the colonization of a wide range of woody and non-woody plants in the understorey (Geldenhuys et al., 1986; Geldenhuys, 1996; Lübbe and Geldenhuys, 1991; Parrotta, 1995a; Van Heerden and Masson, 1991). Sometimes this colonisation is considered as a financial burden,

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such as in commercial plantations (Van Heerden and Masson, 1991). In the South African evergreen forest zone these plantation stands with understorey plants have been successfully converted to facilitate development of native secondary forest (Van Wyk et al., 1995). It is therefore possible to use this process to restore degraded forest or to establish forest on land which has been without forest for a long time.

Native, mixed evergreen forests cover a small area of about 3000 km^2 in South Africa (0.08% of the land surface area) and could not provide in the timber needs for economic development in the country. The native forests occur as scattered patches of many small and a few large forests and are confined to a narrow strip along the eastern margin of southern Africa (between the eastern escarpment and the Indian Ocean). They include both high and scrub forest, occur on a wide range of geological formations, and are limited to areas with mean annual rainfall >525 mm with strong winter rain and >725 mm with strong summer rain (Geldenhuys, 1993; Rutherford and Westfall, 1986). The relic nature of the forests within the fire-prone vegetation types (grassland, shrubland and woodland) resulted primarily from their persistence in topographic shadow areas (refuge sites) in relation to the main fire-bearing winds, i.e. hot, desiccating föhn-like winds (locally known as bergwinds) occurring during winter (Geldenhuys, 1994). Floristically the forests are part of the Afromontane forests (White, 1983) and share many species with forests as far north as Ethiopia (Geldenhuys, 1992).

Afforestation with fast-growing introduced timber species in South Africa was started in 1890 to provide the timber needs of the country (Scholes et al., 1995). Timber plantation area increased rapidly after 1920 to 1.4 million ha in 1993. This includes 671 000 ha planted with pines (mainly *Pinus patula*, *P. elliottii* and *P. taeda* in the summer rainfall areas), 524 000 ha with eucalypts (mainly *Eucalyptus grandis* in summer-rainfall areas), and 104 000 ha planted with wattle (mainly *Acacia mearnsii*). About 40% of the country's forestry plantation area occurs in Mpumalanga Province in the northeastern part of the country where they cover 8% of the province's land surface.

Commercial plantations have both negative and positive impacts on the environment. They use more water than the natural vegetation they replace and therefore affect streamflow to areas outside the high-rainfall mountainous areas. In summer-rainfall areas the plantations were established on high-lying grasslands, in particular along the eastern escarpment. The Mpumalanga montane grasslands are one of the seven biodiversity 'hot spots' in South Africa, containing 1600 plant species of which 113 are endemics (Scholes et al., 1995). Along this escarpment 106 species (86 plant, 6 mammal, 6 bird, 4 fish and 4 reptile species) are considered threatened, largely by forestry practices. In the south of the country plantations were established in areas of biotically highly diverse sclerophyll shrublands. Many plantation tree species readily invade land adjacent to forestry plantations, including riparian habitats, and the plantations also encourage the spread of other invader species.

Plantation forestry contributed to the expansion and recovery of the native forest and the wider distribution of some forest species (see review by Geldenhuys et al., 1986). Species selected for afforestation (such as pines, eucalypts and acacias) were generally easily raised, fast-growing, light-demanding species from rain forest or other sources. The intensive fire protection measures in plantations reduced the frequency of destructive fires near the forest. They also reduced the pressure on the native forests by providing in the timber and fuelwood needs. Very little afforestation was done in cleared forest; only occasionally in forest glades and small clearings. The plantations often facilitate the establishment of shade-tolerant native forest species. Afforestation has also increased the diversity and geographic spread of forest birds (Oatley, 1984). The native forest is also resilient to the invasion by introduced timber and other alien species (Geldenhuys et al., 1986; Geldenhuys, 1996).

A study was conducted in plantation areas adjacent to native, mixed evergreen forest along the escarpment in the Northern Province (north of Mpumalanga Province), as part of a broader project to assess the catalytic effect of tree plantings on the rehabilitation of native forest biodiversity on degraded tropical lands (Parrotta, 1995b). The objectives of this study were to test the following selected hypotheses from the overall project: understorey colonization by indigenous plant species is strongly influenced by the specific species of the overhead plantation; and, abundance and diversity of the indigenous woody and herbaceous species increase with increasing age of the plantation stand.

2. Study area

The Eastern Transvaal escarpment between the towns of Nelspruit and Tzaneen in the Mpumalanga and Northern Provinces (approximately 23°S to 25°S and 30°E to 31°E) is the main commercial plantation area in South Africa. The main plantation species are *Pinus patula*, *P. elliottii*, *P. taeda*, *Eucalyptus grandis* and various other *Eucalyptus* species. The three pine species were planted mainly on the upper cooler and moister part of the gradient, mainly for structural timber on rotations of 30–50 years. On the lower, drier part of the altitudinal gradient and mostly belonging to private timber companies, *E. grandis* is almost the only species planted on shorter rotations of up to 20 years, mainly for poles. The plantations were established in grasslands originally maintained by regular fires. A photograph taken around 1900 on the Woodbush plateau shows the vast grasslands with a small isolated forest patch in a gully (M. Louw, personal communication, 1995). Broad fire breaks are maintained through annual early dry-season burning to protect the plantations against fires. In several areas the plantation tree species have spread and established naturally in the adjacent grasslands as a result of the fire protection measures.

Native forest patches occur mainly on the steep eastern slopes of the Transvaal Escarpment and in deeper valleys, i.e. typical fire refuge sites. They are small in the southern end of the escarpment but cover a large complex in the northern part, i.e. the Woodbush-De Hoek native forest complex (Scheepers, 1978; Cooper, 1985). They cover a gradient from near the top of the cool escarpment to the warm low veld.

Two areas were selected for this study: Woodbush-De Hoek and Entabeni (Fig. 1; Table 1). The plantations selected for the study were established by the State Department of Water Affairs and Forestry (Forestry Branch) and were recently transferred to a timber company, SAFCOL.

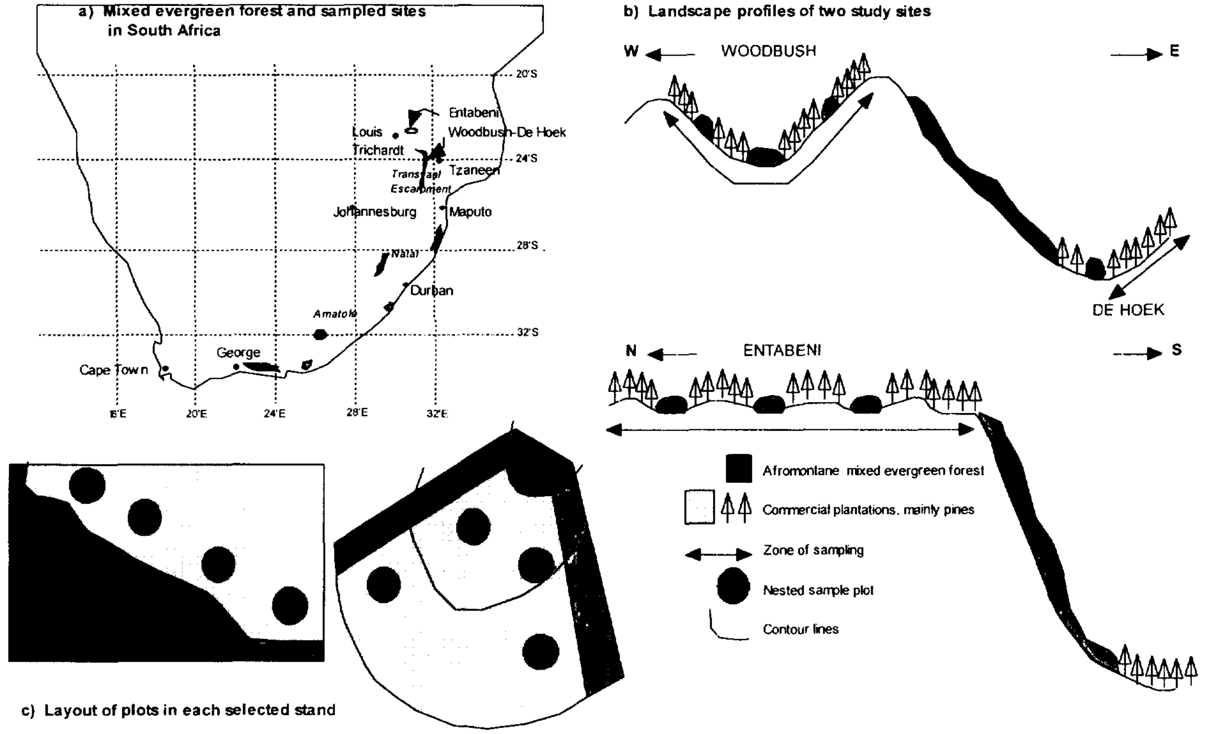

Fig. 1. Distribution of mixed evergreen forest in South Africa and location of study areas in Northern Province, with indication of the landscape profiles of the two study areas and the layout of sample plots in selected stands.

3. Methods

After an initial field reconnaissance of the plantations in Northern Province, it was decided to concentrate on the three pine species on plantations managed by SAFCOL at Woodbush-De Hoek and Entabeni. Only plantation stands adjacent to native forest were selected. Stands which had a recent pruning or thinning were excluded, as well as stands on too steep slopes. A random selection was made of potentially useable sites, and these were then checked in the field before sampling. Control sites in this study were primarily considered to be grassland sites under the natural fire regime. However, it was not possible to find such sites under comparable site conditions within the plantation stands. The two selected sites were unplanted rocky slopes covered in grass with scattered fire-adapted trees, such as *Parinari curatellifolia*.

In each selected site (plantation stand) four plots were sampled in the pine stands (Fig. 1), and two plots each in two small *E. saligna* stands and one small *A. mearnsii* stand. Stand characteristics of the 19 sites sampled in the study are summarised in Table 2. Sixty-six plots were sampled, four of which were sampled on 'control sites'. Nine *Pinus patula* stands (36 plots) were sampled at both Woodbush and Entabeni to test the effect of age of the stand on development of the understorey. Twelve stands were sampled

Table 1

Conditions and characteristics of the three plantation areas selected for the study of native forest regeneration in the understorey of timber plantations in Northern Province, South Africa

Plantation	Woodbush	De Hoek	Entabeni
Location	On plateau above escarpment	Below escarpment, at about mid-level of total altitudinal gradient	On plateau of Soutpansberg mountain complex
Altitude, topography and aspect	1540–1760 m a.s.l.; gentle to fairly steep slopes; variable aspect	1200 m a.s.l.; steep to very steep slopes; variable aspect	1260–1430 m a.s.l.; undulating landscape, with gentle slopes; variable aspect
Geology	Biotite-bearing Archaean granite-gneiss (Visser and Verwoerd, 1960); schistose xenoliths at higher altitudes (Scheepers, 1978)	Biotite-bearing Archaean granite-gneiss (Visser and Verwoerd, 1960)	Basalt in southern part (Block F); mainly quartzitic sandstone in northern part (Blocks G and H) (Louw et al., 1994)
Rainfall	1200 mm $year^{-1}$ in southern end (Block A and B); 1800 mm $year^{-1}$ in northern end (Block G)	1700 mm $year^{-1}$	1960 mm $year^{-1}$ on plateau
Native forest	Small (<10 ha) to medium-sized (<100 ha) patches in gullies; main forest occurs below escarpment to the east	Large, main Woodbush-De Hoek native forest complex on steep slopes below escarpment	Large areas on steeper slopes; small patches in gullies on plateau
Plantation species near forest margin	Mainly *Pinus patula*, *P. elliottii* and *P. taeda*; *Eucalyptus* in few old, small stands, or narrow belts maintained as fire-breaks	Mainly *Pinus elliottii*, *P. taeda* and *P. patula*; *Khaya nyasica* and other introduced tropical hardwoods; *Podocarpus falcatus*, a native timber tree, planted in riparian zones (Geldenhuys and Von dem Bussche, 1997)	*Pinus patula* and *P. taeda*, with some *P. elliottii*, and few old, small stands of *Eucalyptus saligna*
Conditions of plantations	All young stands in second rotation; several older stands adjacent to native forest were recently felled; plantations grow above forest	Plantations grow below forest	Older stands in lower southern end were destroyed by recent devastating fires
Native forest regeneration	Good woody regeneration in older stands in southern part; sparser understorey vegetation in younger stands in northern part	Old stands surrounded by forest with abundant regeneration	Abundant and diverse forest regeneration in southern, lower part; sparser regeneration in northern, higher part

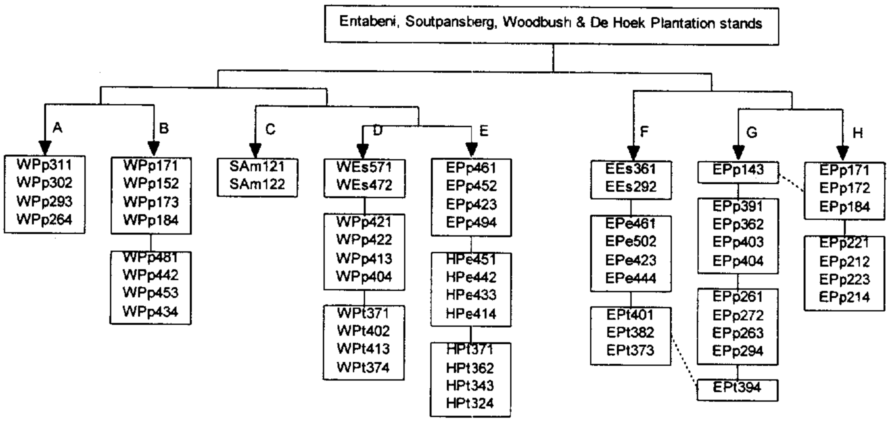

Fig. 2. Results of the TWINSPAN classification of the understorey vegetation on 5-m radius plots in 17 stands of *Pinus*, *Eucalyptus* and *Acacia* in Northern Province, South Africa. Plot codes: E, Entabeni; H, De Hoek; S, Soutpansberg (Hanglip); W, Woodbush; A, *Acacia*; E, *Eucalyptus*; P, *Pinus*; e, *elliottii*; m, *mearnsii*; p, *patula*; s, *saligna*; t, *taeda*. First and second numeral: mean DBH (cm) of canopy trees; Third numeral: plot number in a stand of similar age and management history.

to test the effect of the species in the canopy on the composition of the understorey (24 plots at 6 sites for *P. patula*, 12 plots at 3 sites for *P. taeda*, 8 plots at 2 sites for *P. elliottii*, and 4 plots at 2 sites for *E. saligna*). The stand of *A. mearnsii* was included because of the importance of the species as invader plant in

Table 2

Characteristics of the plantation stands sampled in Entabeni, Woodbush and De Hoek to assess the composition of the regeneration in the understorey

Stand	Code[a]	No. plots	Species	Age (years)	Rotation	Mean value, with standard error between parentheses					
						DBH (cm)	Density (stems/ha)	Basal area (m^2 ha^{-1})	Canopy height (m)	Bole length (m)	Crown cover (%)
Control1	ECa00	2	–	–	–	–	–	–	–	–	–
Control2	ECb00	2	–	–	–	–	–	–	–	–	–
WoodG7d	WPp17	4	*P. patula*	7	2	16.5 (1.0)	756 (57)	16.8 (1.6)	11.3 (0.8)	2.0 (0.1)	71.3 (12.4)
EntF25	EPp17	4	*P. patula*	7	2	16.5 (1.4)	619 (91)	14.7 (4.0)	8.4 (0.6)	3.6 (0.4)	66.3 (4.1)
EntF28a	EPp21	4	*P. patula*	9	2	21.3 (0.5)	606 (133)	23.3 (5.7)	10.9 (2.4)	4.1 (0.4)	66.3 (4.1)
EntH14a	EPp27	4	*P. patula*	14	2	26.8 (1.1)	481 (65)	27.9 (5.4)	21.4 (4.1)	5.0 (1.1)	61.3 (5.4)
WoodG3	WPp29	4	*P. patula*	17	2	29.1 (1.7)	444 (33)	30.0 (2.5)	19.1 (1.4)	6.6 (0.4)	57.5 (11.5)
EntG12	EPp39	4	*P. patula*	31	1	38.6 (1.7)	269 (48)	33.7 (8.0)	27.5 (0.9)	15.5 (3.0)	51.3 (2.2)
WoodB1	WPp41	4	*P. patula*	23	1	41.2 (1.0)	425 (40)	58.4 (3.2)	29.8 (1.9)	14.5 (1.1)	50.0 (5.0)
WoodB5	WPp45	4	*P. patula*	21	2	44.9 (1.9)	306 (57)	50.0 (10.8)	30.1 (2.1)	19.1 (1.4)	50.0 (3.5)
EntF23	EPp46	4	*P. patula*	41	1	45.7 (2.5)	263 (28)	44.3 (3.9)	32.0 (0.7)	21.3 (0.8)	55.0 (3.5)
HoekB9	HPe43	4	*P. elliottii*	35	1	43.3 (1.3)	300 (18)	44.7 (2.7)	28.8 (1.9)	17.3 (1.6)	47.5 (4.3)
EntF24a	EPe45	4	*P. elliottii*	41	1	45.3 (3.1)	306 (37)	50.8 (8.1)	25.3 (0.8)	18.8 (0.8)	58.8 (2.2)
HoekB8a	HPt35	4	*P. taeda*	21	1	34.6 (1.9)	500 (56)	47.4 (3.1)	22.5 (0.9)	6.8 (0.8)	63.8 (4.1)
EntG17	EPt38	4	*P. taeda*	29	1	38.3 (1.3)	406 (37)	47.5 (5.5)	32.8 (0.8)	14.1 (2.4)	60.0 (3.5)
WoodA9c	WPt39	4	*P. taeda*	23	2	38.6 (1.7)	406 (21)	49.1 (6.7)	25.8 (0.4)	11.5 (1.1)	58.8 (4.1)
EntF48	EEs32	2	*E. saligna*	77	1	32.1 (3.5)	438 (38)	61.4 (1.8)	28.5 (2.5)	12.5 (3.5)	57.5 (12.5)
WoodAEuc	WEs52	2	*E. saligna*	90	1	52.3 (4.9)	313 (63)	90.7 (11.2)	>50.0 (0.0)	43.5 (4.0)	50.0 (10.0)
HanWatl	SAm12	2	*A. mearnsii*	20	1	11.7 (0.1)	1275 (200)	17.3 (3.2)	13.5 (1.5)	5.0 (1.0)	60.0 (5.0)

[a]E = Entabeni, H = De Hoek, S = Hanglip in Soutpansberg, W = Woodbush; A = Acacia, E = Eucalyptus, P = Pinus; e = elliottii, m = mearnsii, p = patula, s = saligna, t = taeda. Numerals indicate mean DBH of the stand in cm.

many areas, but the site is on an exposed ridge, and conditions in the stand indicated that the understorey vegetation was severely affected by the recent drought.

Circular plots were used and all plot mid-points were between 15 m and 25 m away from the forest margin. In each plot the following data were recorded in nested subplots centred on plot mid-points: (a) 11.3 m radius for sampling trees of the overhead stand: diameter at breast height (1.3 m) or DBH of all trees; canopy height and clean bole length of four trees near the centre; estimated canopy crown density (%); aspect and slope of the site; (b) 5 m radius for sampling all understorey vegetation: all understorey plants by species and cover %, total cover % of woody plants, graminoids, ferns, other herbs (or forbs), litter, bare soil, and stones, using Braun-Blanquet cover abundance values of *r* (<0.1%), +(0.1–1%), 1 (1–5%), 2 (6–25%), 3 (26–50%), 4 (51–75%), and 5 (>75%); recording of species, height and DBH of all stems ≥2 m height. General notes were made of woody regeneration occurring in the area but not recorded on the plot, signs of animal activity in the area and other relevant information.

A multivariate approach was used in the initial data analyses because of the variability of the different sites (and stands) and understorey species composition in the range of stand ages and plantation species used. The percentage cover of species on the 5-m radius plots were subjected to TWINSPAN (TWo-way INdicator SPecies Analysis of Hill (1979)) to classify the understorey vegetation of the individual plots. Canonical Correspondence Analysis (CCA) (Ter Braak, 1988) was used to relate understorey composition to the overhead stand variables.

4. Results

4.1. Characteristics of the sampled stands

The characteristics of the plantation stands (Table 2) show wide ranges in the different variables sampled for the *P. patula* stands. The variables were, however, relatively similar among the *Pinus* stands of different species and more than 30 cm DBH. These results suggested that one could expect differences in the understorey across the age differences in the *P. patula* stands, and that differences in understorey vegetation among the older stands of the different species could be attributed to plantation species effects.

However, no significant correlations were calculated between stand characteristics and the cover of different components of the understorey. Most stands had no bare soil and only three had > 25% bare soil (only the *A. mearnsii* stand, one control plot, and one young *P. patula* plot at Entabeni). Very few plots had exposed stones of more than 5% cover in the understorey, except for one control plot (>25%). Most plots had a high cover of bare litter (>50%), even with a good cover of woody regeneration or ferns. There seems to be an inverse relationship between grass cover and cover of bare litter, but the relationship is not significant.

Cover of woody regeneration (of all sizes) varied from very low (no zero occurrences) to almost 50% of the plots with more than 50% cover, but the relationship with stand characteristics, such as mean DBH and mean clean bole length, for the age range within *P. patula*, was not significant. Similarly, in an analysis of variance, the differences in cover of woody regeneration among different canopy species of the older stands were insignificant. Woody regeneration, ferns, grasses and herbs often occurred in clumps, which meant that the same plot may have good cover (>25%) of all these categories.

4.2. Classification and ordination of understorey communities

The visual assessment suggested that, although the cover abundance of woody regeneration between stands may not be different, the species composition may be different. For most stands all the sampled plots from a specific stand clustered in the same TWINSPAN classification category (Fig. 2) which suggested that despite variable conditions within a stand, the same species occurred scattered throughout the stand. No single species was particularly prominent in separation of the plots into the groups. It seems that loose assemblages of species that were present in some of the plots contributed to the groupings. Only two Entabeni plots did not group together with the other plots of a stand.

The main subdivision separated the Woodbush-De Hoek and *A. mearnsii* plots from the Entabeni plots.

The exception was one old Entabeni stand of *P. patula* which grouped with the Woodbush-De Hoek stands, in particular the De Hoek stands (group E, all with very good tree regeneration). In the Woodbush-De Hoek group the older stands (groups D and E) separated from the younger stands (groups A and B), except for one old stand of *P. patula* (in group B) which contained very little understorey vegetation. The old *Eucalyptus* stand grouped with the old stands of the three *Pinus* species, in particular group D, all with very good tree regeneration. The *A. mearnsii* stand (group C) was isolated from the other stands. The Entabeni stands separated into three groups: group F with old stands of *Eucalyptus*, *P. elliottii* and *P. taeda*; group G with older stands of *P. patula* combined with isolated plots of other stands; and group H with the younger *P. patula* stands.

In general, the results of the classification suggest that the composition of the woody regeneration is different between the two main study areas. In both study areas, the species composition differs between stands of different age within *P. patula*, but that within a site, such as Woodbush southern part or at De Hoek, species composition is similar between older stands of different species.

Interpretation of the ordination diagram of CCA, i.e. a linear unimodal direct gradient analysis, of the woody regeneration (Fig. 3) is done according to Ter Braak (1986) and Jongman et al. (1987). The plot scores (or mean stand scores as indicated on the diagram) are parameters of unimodal response curves of species. Species scores are not indicated here. Stand scores are represented by points and environmental variables by an arrow for continuous variables and a point for nominal variables (the point is a centroid or weighted average of the sites belonging to that class). Each arrow determines an axis in the diagram. The position of a stand approximates the weighted average of a stand as a deviation from the grand mean of each of the environmental variables. For interpretation of the relationship between a stand and an environmental variable, the stand point must be projected onto that environmental axis. The inferred weighted average is higher than average of the environmental variable if

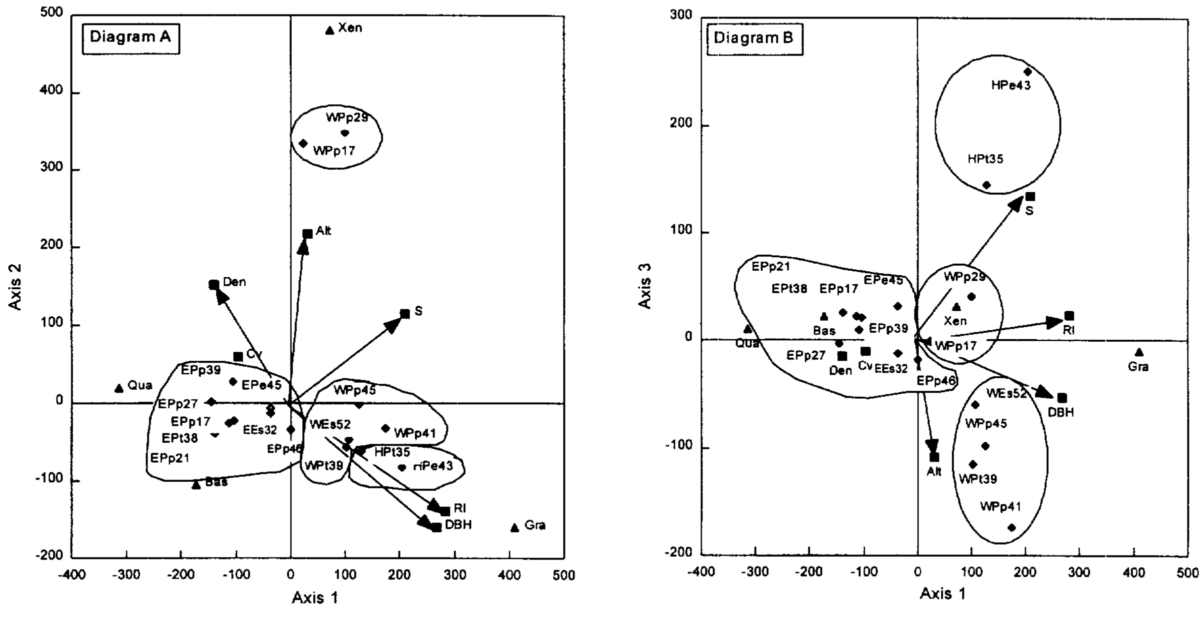

Fig. 3. Results of the CANOCO CCA ordination of the woody regeneration in the understorey on 5-m radius plots in 16 stands of *Pinus* and *Eucalyptus* in Northern Province, South Africa. Diagram A displays the plots and environmental variables in relation to axes 1 and 2, and diagram B displays them for axes 1 and 3. Stand codes: E = Entabeni; H = De Hoek; W = Woodbush; E = Eucalyptus; P = Pinus; e = elliottii; p = patula; s = saligna; t = taeda. First and second numeral: mean DBH (cm) of canopy trees. The continuous environmental variables, indicated by a square, are Alt = Altitude; DBH = mean stand DBH; Den = stand density; RI = radiation index; S = slope. Geology is analysed as nominal variables and indicated as triangles, and are as follows: Bas = Basalt; Gra = Granite-gneiss; Qua = Quartzite; Xen = Schistose xenoliths in granite-gneiss.

the projection lies between the origin and the arrow head, and is lower than average if the origin lies between the projection point and arrow head. Environmental variables with long arrows are more strongly correlated with the ordination axes than those with short arrows, and therefore more closely related to the pattern of variation in species composition.

The *A. mearnsii* stands were excluded from this analysis because they were extreme outliers in an initial analysis. The stands grouped into four clusters (Fig. 3): the two young Woodbush *P. patula* stands at high altitude on schistose xenoliths; the other older Woodbush stands of different canopy species; the two De Hoek stands of different canopy species; and all the Entabeni plots together in one large cluster. The three axes explained 57% of the variance (axis 1 = 22.3%; axis 2 = 17.8%; axis 3 = 16.9%). Axis 1 (Eigenvalue 0.569) separated the Woodbush-De Hoek stands from the Entabeni stands. It is best correlated with granite-gneiss ($r = 0.828$) and quartzite ($r = -0.637$) at two extremes, radiation index ($r = 0.568$), mean stand DBH ($r = 0.538$) and slope ($r = 0.422$). Axis 2 (Eigenvalue 0.454) separated the two young Woodbush Block G *P. patula* stands from all the other stands. It is best correlated with schistose xenolith ($r = 0.966$) and altitude ($r = 0.438$). Axis 3 (Eigenvalue 0.432) separated Woodbush Block A older stands of different canopy species from the De Hoek older stands (at the extremes), with all the Entabeni stands and the two young Woodbush Block G stands in the middle. It is best correlated with slope ($r = 0.271$) and

Table 3

Total number of species per growth form and mean number (and standard error of mean) of species per 5-m radius plot for different growth forms in pine, eucalypt and acacia stands in Northern Province, South Africa. See Fig. 2 for grouping of stands in the classification dendrogram

Growth form	Number of species		Statistic	Classification category (see Fig. 2[a])							
	Total	Aliens		A WPp29	B WPp17 WPp45	C SAm12	D WEs52 WPp41 WPt39	E EPp46 HPe43 HPt35	F EEs32 EPe45 EPt38	G EPp39 EPp27	H EPp17 EPp21
Canopy trees	32	6	Mean	4.0	2.5	1.5	3.7	4.0	2.6	2.5	2.4
			SE	2.1	2.1	1.5	1.3	1.7	1.2	1.1	1.4
Sub-canopy trees	30	0	Mean	2.0	0.3	1.5	2.8	1.9	2.2	1.5	2.1
			SE	1.9	0.4	0.5	1.1	1.4	1.4	1.3	1.5
Woody shrubs	13	2	Mean	1.3	1.3	0.5	0.9	0.5	0.6	1.5	1.0
			SE	0.8	1.1	0.5	0.9	0.5	0.7	0.7	0.5
Soft shrubs	7	0	Mean	0.5	0.1	0.5	0.4	0.3	0.6	0.9	1.0
			SE	0.5	0.3	0.5	0.5	0.5	0.7	0.3	0.0
Lianes	17	1	Mean	0.3	0.5	2.0	1.9	2.1	1.7	1.1	2.4
			SE	0.4	0.7	1.0	0.7	1.0	1.3	1.3	1.2
Vines	13	0	Mean	0.3	0.8	–	1.1	0.4	0.2	0.6	0.6
			SE	0.4	0.4	–	0.8	0.5	0.4	0.7	0.7
Ferns	13	0	Mean	2.3	2.3	–	1.5	1.7	1.1	2.4	1.3
			SE	1.9	1.0	–	0.9	0.6	0.7	1.0	0.7
Graminoids	15	0	Mean	1.8	2.5	0.5	3.3	3.0	2.1	1.0	1.5
			SE	0.4	0.9	0.5	0.9	1.1	0.8	1.0	0.9
Geophytes	11	0	Mean	0.8	–	1.0	1.3	0.5	0.1	–	0.4
			SE	0.8	–	0.0	1.2	0.5	0.3	–	0.5
Herbs/forbs	19	0	Mean	2.5	1.1	0.5	2.0	1.1	0.3	0.6	0.8
			SE	1.1	1.2	0.5	1.9	0.9	0.5	0.7	1.0
Total	170	9	Mean	15.5	11.3	8.0	18.9	15.5	11.5	12.1	13.4
			SE	5.9	3.5	3.0	3.9	4.6	3.7	3.8	3.2

[a]Stands included in each category: E = Entabeni, H = De Hoek, S = Hanglip in Soutpansberg, W = Woodbush; A = Acacia, E = Eucalyptus, P = Pinus; e = elliottii, m = mearnsii, p = patula, s = saligna, t = taeda. Numerals indicate Mean DBH of the stand in cm.

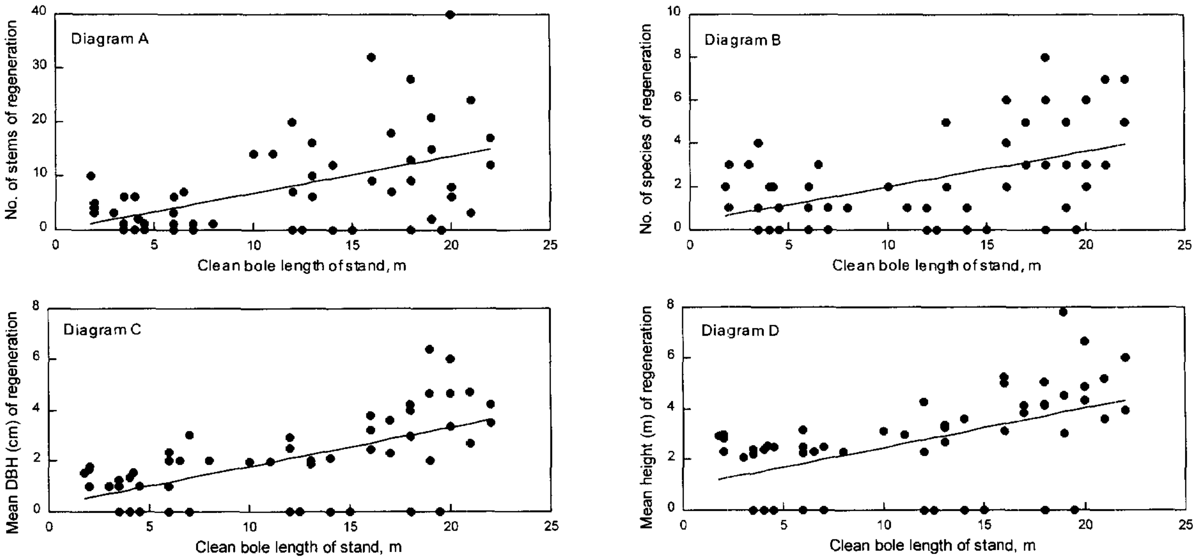

Fig. 4. Relationship between overstory mean bole length and understory woody regeneration parameters in pine plantations in the Northern Province, South Africa. (A) Regeneration density (No. stems): $Y = 0.6863X - 0.1295$; SE (Y est) = 7.747; $r^2 = 0.257$; df = 54; $P < 0.01$; (B) Species richness: $Y = 0.3211 + 0.1657X$; SE (Y est) = 1.857; $r^2 = 0.259$; df = 54; $P < 0.01$; (C) Mean DBH of regeneration: $Y = 0.2235 + 0.1543X$; SE (Y est) = 1.308; $r^2 = 0.380$; df = 54; $P < 0.01$; (D) Mean regeneration height: $Y = 0.8997 + 0.6863X$; SE (Y est) = 1.648; $r^2 = 0.282$; df = 54; $P < 0.01$.

altitude ($r = -0.219$), but the correlations are not very strong. In general the results suggest that site conditions affected the composition of the woody understorey more than the age of a stand within *P. patula*, or the canopy species of the older stands.

4.3. Floristic and structural composition of understorey vegetation

A total of 170 species were recorded from the 62 plots, and include all the major growth forms represented in the surrounding forest, except for the epiphytic flora. Total number of species per growth form and mean number of species per plot in a site are indicated for each of the classification categories by 10 growth forms (Table 3). The best represented group is canopy trees with 32 species followed by sub-canopy trees with 30 species. Woody plants include 92 species (54% of all species). Nine introduced species, mainly canopy tree species, were recorded.

Species richness, i.e. absolute number of species, shows great variation between different stands, even within the same group of the classification (Table 3). No clear pattern of species richness emerges from the different stands. Analyses of variance were calculated for the number of species of the woody regeneration, of the herbaceous understorey vegetation and for all

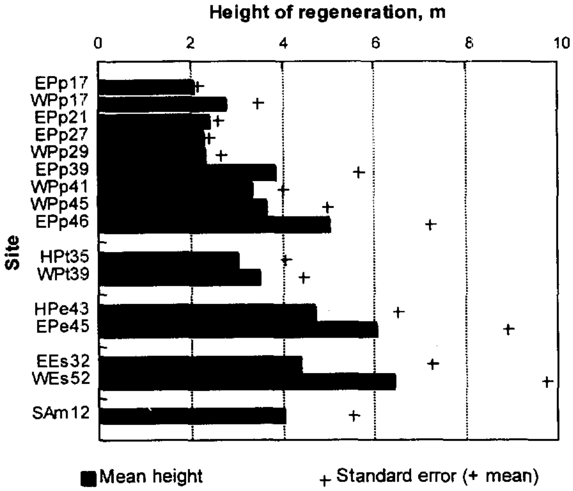

Fig. 5. Mean height (and standard error) of woody regeneration in stands of pine, eucalypt and acacia plantations in Northern Province, South Africa. Stand codes: E, Entabeni; H, De Hoek; S, Soutpansberg (Hanglip); W, Woodbush; A, *Acacia*; E. *Eucalyptus*; P, *Pinus*; e, *elliottii*; m, *mearnsii*; p, *patula*; s, *saligna*; t, *taeda*. Numerals indicate mean DBH (cm) of canopy trees.

Table 4

List of species by growth forms with an occurrence of 10% or more of all the understorey plots in pine or eucalyptus plantation stands in Northern Province, South Africa

Species	Frequency (%)	Mean BB[a] cover
Canopy trees		
Croton sylvaticus	43.5	1.0
Rapanea melanophloes	40.3	0.6
Combretum kraussii	30.6	1.5
Xymalos monospora	30.6	1.3
Syzygium guineense	21.0	0.5
Pinus patula	17.7	1.0
Nuxia floribunda	16.1	0.8
Nuxia congesta	11.3	0.7
Sub-canopy trees		
Ochna arborea	24.2	0.9
Maesa lanceolata	24.2	0.8
Aphloia theiformis	12.9	1.4
Peddiea fischeri	11.3	0.7
Woody shrubs		
Rubus spp.	25.8	0.6
Clutia pulchella	22.6	0.9
Myrsine africana	12.9	1.7
Soft shrubs		
Plectranthus sp.	41.9	1.6
Woody climbers (lianes)		
Canthium gueinzii	35.5	0.5
Smilax kraussiana	24.2	0.6
Senecio deltoideus	22.6	0.9
Clematis brachiata	22.6	0.8
Secamone alpini	17.7	0.5
Herbaceous climbers (vines)		
Vine sp1	19.4	0.6
Vine sp6	11.3	0.9
Ferns		
Pellaea viridis	54.8	0.6
Pteridium aquilinum	17.7	1.6
Thelypteris interrupta	17.7	1.0
Asplenium aethiopicum	16.1	0.9
Asplenium simii	14.5	0.4
Graminoids		
Setaria megaphylla	37.1	1.0
Cyperus sp1	32.3	1.8
Cyperus sp2	30.6	0.8
Oplismenus hirtellus	30.6	2.1
Schoenoxiphium sp.	27.4	0.6
Ehrharta sp.	14.5	1.7
Geophytes		
Protasparagus sp.	19.4	0.7
Herbs/forbs		
Galopina circaeoides	37.1	0.7
Impatiens hochstetteri	11.3	0.9

[a]Braun–Blanquet cover scale.

species in a plot. All differences were not significant: between the different species of stands with DBH of 35 cm or more; between stands of different age of *P. patula*; and between the categories of the TWINSPAN classification. Most of the growth forms are represented in all stands. Geophytes and vines are most poorly represented. The highest mean number of species per 5 m radius plot in a stand (22.5 species) was recorded for the *P. taeda* stand in Woodbush. The old stands at Woodbush and De Hoek had a high mean number of species per plot, generally higher than those at Entabeni (except one 46-year-old *P. patula* stand which had 18.8 total species and 8.8 tree species per plot). Very few woody species occur in more than 10% of the plots (7 canopy trees, 4 sub-canopy trees and 3 woody shrubs). Twenty-five canopy tree species, 26 sub-canopy tree species and 10 woody shrub species occur in 10% or less of the plots.

A total of 38 species occurred in 10% or more of the plots in the pine and eucalypt stands (Table 4). Only one species, the fern *Pellaea viridis*, occurred in more than 50% of the plots. Four canopy tree species occur with a frequency of 30% and more: *Croton sylvaticus* (which was only present in the Entabeni and De Hoek stands), *Rapanea melanophloeos* (the most widespread tree species), *Combretum kraussii* and *Xymalos monospora*.

4.4. Woody regeneration

Linear regression analysis was used to assess the relationship between woody regeneration ≥2 m height (stem density, mean DBH, mean height and number of species) and variables of the overhead plantation stand (stem density, stand height, stand DBH and

Table 5

Propagule types of trees, shrubs and climbers in the regeneration under plantation stands in the Northern Province, South Africa

Growth form	Propagules dispersed by animals		Dry propagules generally not dispersed by animals	
	Species widespread in study area (≥10% frequency)	Species with occasional to rare occurrence (<10% frequency)	Species widespread in study area (≥10% frequency)	Species with occasional to rare occurrence (<10% frequency)
Canopy trees	3	19	5	5
Sub-canopy trees	5	20	0	1
Woody shrubs	3	5	0	5
Lianes	2	5	3	4
Vines	0	6	0	4
Total	13	55	8	19

clean bole length). Clean bole length, which increases with stand age, gave the best regression coefficients for the four regeneration variables ($r^2 = 0.26–0.38$, $P < 0.01$, Fig. 4). Although several plots throughout the stand age range contained no regeneration ≥2 m height, the general trend is for an increased species richness, stem density, and size of plants of woody regeneration with increasing stand age.

The range in height of the woody regeneration varied much in the different stands (Fig. 5). The *P. patula* stands had relatively sparse and small woody regeneration at Woodbush, but had dense and tall woody regeneration in the older stands of Entabeni. The younger stands, at both Woodbush and Entabeni, had sparse and short woody regeneration. The old stands of *P. elliottii* had dense and tall woody regeneration at both De Hoek and Entabeni. The two *E. saligna* stands had dense and tall woody regeneration. The Entabeni stand had particularly dense shorter woody stems, which could be attributed to the many stems of *Cinnamomum camphora*, and the direct exposure on all sides of the relatively small stand. In some stands the high density of stems, some of which were shorter than 2 m, resulted from the clearing of the understorey vegetation. Most of the species show a strong ability to sprout or coppice after cutting.

The recorded woody species show two major seed dispersal strategies. Many species have fleshy fruits, or have seeds with fleshy attachments. These usually attract birds, bats or other animals (such as primates). Other species have dry fruits such as capsules, pods or other structures with small seeds or seed with attachments which allow the seed to be carried by wind. Some seeds are released through ballistic mechanisms. Table 5 shows the dispersal syndromes for the trees, shrubs and climbers recorded in the study, and are based on personal knowledge, observation in the study areas or descriptive notes of the species (from Palgrave, 1977). A few unidentified species were excluded from the analyses because the type of fruit or seed was unknown. The majority of the tree, shrub and climber species are animal-dispersed. Only 24% of the animal-dispersed species have widespread occurrence compared to 42% of the species with dry propagules. The tree species recorded in the study are listed in Table 6, by propagule type. The absolute frequency of occurrence is indicated for each species. It shows that a large number of species from the forest have been carried into the plantations, either by wind, animals or other unknown means.

Various signs of animals moving around in the plantation stands were observed. For example, footprints, faeces and browsing indicated the presence of bushpig (*Potamochoerus porcus*), bushbuck (*Tragelaphus scriptus*) and baboon (*Papio ursinus*). Seedlings of species with fleshy fruit were found to be concentrated around the base of large trees, indicating that the dispersers may have been perching in the crowns of those trees. Plants of wind-dispersed species were found to be more scattered throughout a plantation stand. During the study many birds (frugivores, insectivores, nectarivores and birds of prey) as well as of two other primates, Samango monkey (*Cercopithecus mitis*) and Vervet monkey (*Cercopithecus aethiops*) were identified by their calls.

Table 6

Frequency of occurrence and propagule types of tree species recorded from the understorey regeneration in pine, eucalypt and acacia plantation stands on the forest margin in Northern Province, South Africa

Canopy trees		Sub-canopy trees	
'Fleshy' propagules dispersed by animals			
Rapanea melanophloeos	26[a]	*Ochna arborea*	16
Xymalos monospora	19	*Maesa lanceolata*	14
Syzygium guineense	14	*Aphloia theiformis*	13
Acacia melanoxylon[b]	6	*Canthium ciliatum*	7
Cussonia spicata	5	*Peddiea fischeri*	7
Kiggelaria africana	5	*Ochna holstii*	5
Zanthoxylum davyi	4	*Rhus spp2*	5
Syzygium cordatum	3	*Tree spp3*	5
Rhus chirindensis	2	*Bersama transvaalensis*	4
Schefflera umbellifera	2	*Halleria lucida*	4
Apodytes dimidiata	1	*Tricalysia lanceolata*	4
Celtis africana	1	*Euclea natalensis*	3
Cinnamomum camphora[b]	1	*Maytenus acuminata*	3
Cryptocarya liebertiana	1	*Maytenus mossambicensis*	3
Drypetes gerrardii	1	*Trimeria grandifolia*	3
Ilex mitis	1	*Bequartiodendron magalismontanum*	2
Maytenus peduncularis	1	*Euclea divinorum*	2
Olea capensis	1	*Eugenia natalitia*	2
Pittosporum viridiflorum	1	*Heteropyxis natalensis*	2
Psydrax obovata	1	*Peddiea africana*	2
Scolopia zeyheri	1	*Clausena anisata*	1
Vepris lanceolata	1	*Psychotria zombamontana*	1
		Rhus spp1	1
		Scutia myrtina?	1
		Tricalysia capensis	1
'Dry' propagules generally not dispersed by animals			
Croton sylvaticus	27	*Buddleja salviifolia*	1
Combretum kraussii	21		
Pinus patula[b]	11		
Nuxia floribunda	9		
Nuxia congesta	8		
Brachylaena discolor	6		
Eucalyptus grandis[b]	4		
Pinus elliottii[b]	2		
Pinus taeda[b]	2		
Homalium dentatum	1		

[a] Number of plots in which the species was present (62 plots were sampled).

[b]Introduced species.

5. Discussion

5.1. Catalytic effect of tree plantations

The study has clearly shown that a large number of native forest species establish in the understorey of plantation stands near the forest margin. A total of 170 species of all the plant growth forms occurred, of which 62 were tree species. There is also a tendency for the woody regeneration to increase in species richness, stem density, height, and stem diameter with increasing age of the stand. The study therefore supports the second hypothesis, i.e. that abundance and diversity of the native woody species increase with increasing age of the plantation stand. However, relatively young stands contained some woody forest species. These may have persisted through vegetative regrowth after clearfelling the stands of the first rotation. Some older stands had very good regeneration such as stand WoodB1, whereas others in the same area had very sparse regeneration such as stand WoodB5.

The first hypothesis, i.e. that understorey colonisation of native species is strongly influenced by the specific canopy species, was not supported by the study. Results presented in Fig. 5 suggest that the canopy species may have an effect on the composition, density and size of the regeneration, but results of the classification and ordination analyses do not support this. Results of the CCA ordination suggest that site conditions such as substrate (geology representing nutrient status and drainage) and temperature (altitude and radiation index representing temperature) had a stronger influence on understorey woody regeneration. The sampled stands at Entabeni Block F (on basalt) generally had better regeneration than the stands at Entabeni Blocks G and H (on quartzites). In the Woodbush-De Hoek complex all the sampled stands grow on the granite-gneiss, with some xenoliths enclosed at the higher parts of Block G. The reason for the better regeneration in general at De Hoek and Woodbush Blocks A and B may be the higher temperature at this level than at the higher-lying parts of Woodbush Block G.

Another possible factor is the amount and quality of light in the understorey. The light conditions in a stand change as the stand grows taller. Tree height and crown density and volume become more variable, and gaps of variable shape and size start to develop. These conditions were not easy to assess, but woody regeneration, ferns, graminoids or a combination of these sometimes occurred in denser and taller clumps where the crown appeared less dense, or near the plantation edge where light penetrated from the side. This may be the reason why the clear bole length correlated well with the four variables of good woody regeneration (Fig. 4).

The presence in the area of more aggressive forest regrowth species such as *Croton sylvaticus* at De Hoek and Entabeni and *Aphloia theiformis* at Entabeni may be another contributing factor. Stand management history is another influential factor. The understorey vegetation in parts of the plantations have been cut or treated with herbicide to reduce the fire hazard. In some stands such as at WoodA9c and WoodB1 it was clear from the way the regeneration formed multiple stems on a cut base that the regeneration had been slashed some years before. Other stands such as EntF23 and WoodAEuc show no signs of slashing of the understorey.

5.2. Potential for application

Although the results were not clear on factors controlling establishment in the understorey by native forest flora, the results demonstrate a useful successional process which could be employed to achieve specific objectives at relatively low costs. A better understanding of the controlling factors is needed to manipulate the process to our benefit. Geldenhuys (1995) proposed a modelling approach based on the multiple regression with understorey density, floristic composition (species diversity) and development as dependent variables, and the changing characteristics of the overhead stand and associated microsite variables such as light intensity, pH, organic matter and soil moisture as independent variables. Such a model could indicate different options for stand management.

If weed control in a plantation stand is the objective, it may be necessary to grow stands at a higher density with possible reduced weed control costs but possibly some loss of timber volume.

If abandoned plantation stands or stands of invader plants have to be converted to natural forest, for example in riparian zones or on the forest margin, a thinning regime could be developed to favour establishment of shade-tolerant species without allowing the re-establishment of invader plant species. For example, Van Wyk et al. (1995) summarised results from various studies where native forest is restored by manipulation (careful thinning) of plantation stands on the edge of the forest. The native forest tree regeneration developed into diverse secondary forest with many of the canopy tree species of the neighbouring forest well represented. In a similar way, commercial plantation trees could be planted in areas allocated for restoration, to provide interim financial returns while the area is restored. Introduced species as in this study, or suitable and useful native species such as the native timber tree *Podocarpus falcatus*

(Geldenhuys and Von dem Bussche, 1997), could be used.

If a particular crop has to be grown in the understorey, a suitable thinning regime could be developed to suit optimum growth of that crop species in the understorey. For example, *Rumohra adiantiformis*, a native fern used as florist's greenery (Geldenhuys and Van der Merwe, 1988), was successfully grown in the understorey of mature pine stands. The principles used for the production of the fern has been used in agroforestry and taungya systems to increase production in relatively small areas of community land, such as the damar model with *Shorea javanica* (de Foresta and Michon, 1994).

5.3. Recommendations for future research

The present study has indicated the potential of using the catalytic effect of plantation stands to restore native biodiversity on degraded land. However, this study has had many weaknesses due to the diverse site conditions and the lack of suitable comparable sites. It is recommended that further studies be conducted that examine: (i) the manipulation of young plantation stands using an experimental design to control for some variables while testing for the effect of others; (ii) the economic costs involved to achieve specific objectives, and the socio-economic benefits that could be derived from the system; (iii) the potential of different applications using an adaptive management research approach in which entrepreneurs would be asked to apply the system, with the effects, costs and benefits monitored in order to further improve the systems.

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