# La richesse spécifique peut-elle être conservée dans des forêts exploitées d'Acacia heterophylla, espèce endémique de l'île de la Réunion (Océan Indien) ?

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# Can species richness be maintained in logged endemic *Acacia heterophylla* forests (Réunion Island, Indian Ocean) ?

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**Abstract**

It is assumed that forests can serve multiple uses, including wood production and maintenance of high biodiversity level. We tested this hypothesis by studying eradication methods of invasive plants currently implemented in exploited endemic *Acacia heterophylla* forests located in a tropical highland forest region on the island of Réunion. We also compared species richness in logged (over time) and natural forests. Our results show that all individuals of the widespread alien invasive plant *Rubus alceifolius* were generated from cuttings. We quantified the high growth capability of this species by comparing with those of *Acacia heterophylla* along with *Rubus apetalus* var. *apetalus*, a close non-invasive congener. The substantial multiplicative and vegetative growth ability of *R. alceifolius* enabled it to form monospecific patches in only 2.5 years. The species richness of the exploited *Acacia heterophylla* forest was thus very affected. Although the species richness increased over time after logging, the extent of the resulting richness was not as great as that in natural forests which, moreover, included numerous exotic plants. The authors assess the impact of highly disturbing logging operations and, based on the results of the comparisons, are very pessimistic about the possibility of maintaining species richness in logged forests. Nevertheless, the results indicate that the situation is not beyond hope and an eradication program specifi cally tailored to this kind of forest is proposed if exploitation will stop.

**Résumé**

*La richesse spécifique peut-elle être conservée dans des forêts exploitées d'Acacia heterophylla*, espèce endémique de l'île de la Réunion (océan Indien) ? – Il est globalement considéré que les forêts peuvent assurer des usages multiples, incluant la production de bois et le maintien d'un niveau élevé de biodiversité. Dans le but de tester cette hypothèse, nous avons étudié les méthodes d'éradication de *Rubus alceifolius* actuellement utilisées au sein d'une forêt exploitée d'*Acacia heterophylla*, espèce endémique de l'île de la Réunion. Nos résultats montrent que tous les individus de l'espèce envahissante la plus répandue dans la zone -*Rubus alceifolius*-, proviennent de bouturage. Nous avons aussi quantifié la forte capacité de croissance de cette espèce au travers d'une comparaison de croissance avec l'Acacia heterophylla mais aussi avec un congénère indigène -*Rubus apetalus* var. *apetalus*. Ces capacités de multiplication et de croissance végétatives importantes permettent à Rubus alceifolius de former des massifs monospécifiques en seulement 2,5 ans. La richesse spécifique de la forêt d'*Acacia heterophylla* exploitée en est alors largement affectée. En effet, de manière générale, même si la richesse spécifique semble augmenter légèrement au cours du temps, les espèces observées sont généralement des espèces exotiques envahissantes. Comparant l'extraction du bois à un haut niveau de perturbation, les auteurs sont très pessimistes sur la possibilité de maintenir une diversité spécifique élevée au sein d'une forêt exploitée. Néanmoins ces résultats apportent une lueur d'espoir et un programme d'éradication mieux adapté au type de forêt étudié est proposé.

# CAN SPECIES RICHNESS BE MAINTAINED IN LOGGED ENDEMIC *ACACIA HETEROPHYLLA* FORESTS (RÉUNION ISLAND, INDIAN OCEAN)?

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RÉSUMÉ. — *La richesse spécifique peut-elle être conservée dans des forêts exploitées d'*Acacia heterophylla, *espèce endémique de l'île de la Réunion (océan Indien) ?* – Il est globalement considéré que les forêts peuvent assurer des usages multiples, incluant la production de bois et le maintien d'un niveau élevé de biodiversité. Dans le but de tester cette hypothèse, nous avons étudié les méthodes d'éradication de *Rubus alceifolius* actuellement utilisées au sein d'une forêt exploitée d'*Acacia heterophylla*, espèce endémique de l'île de la Réunion. Nos résultats montrent que tous les individus de l'espèce envahissante la plus répandue dans la zone -*Rubus alceifolius*-, proviennent de bouturage. Nous avons aussi quantifié la forte capacité de croissance de cette espèce au travers d'une comparaison de croissance avec l'*Acacia heterophylla* mais aussi avec un congénère indigène -*Rubus apetalus* var. *apetalus*. Ces capacités de multiplication et de croissance végétatives importantes permettent à *Rubus alceifolius* de former des massifs monospécifiques en seulement 2,5 ans. La richesse spécifique de la forêt d'*Acacia heterophylla* exploitée en est alors largement affectée. En effet, de manière générale, même si la richesse spécifique semble augmenter légèrement au cours du temps, les espèces observées sont généralement des espèces exotiques envahissantes. Comparant l'extraction du bois à un haut niveau de perturbation, les auteurs sont très pessimistes sur la possibilité de maintenir une diversité spécifique élevée au sein d'une forêt exploitée. Néanmoins ces résultats apportent une lueur d'espoir et un programme d'éradication mieux adapté au type de forêt étudié est proposé.

SUMMARY. – It is assumed that forests can serve multiple uses, including wood production and maintenance of high biodiversity level. We tested this hypothesis by studying eradication methods of invasive plants currently implemented in exploited endemic *Acacia heterophylla* forests located in a tropical highland forest region on the island of Réunion. We also compared species richness in logged (over time) and natural forests. Our results show that all individuals of the widespread alien invasive plant *Rubus alceifolius* were generated from cuttings. We quantified the high growth capability of this species by comparing with those of *Acacia heterophylla* along with *Rubus apetalus* var. *apetalus*, a close non-invasive congener. The substantial multiplicative and vegetative growth ability of *R. alceifolius* enabled it to form monospecific patches in only 2.5 years. The species richness of the exploited *Acacia heterophylla* forest was thus very affected. Although the species richness increased over time after logging, the extent of the resulting richness was not as great as that in natural forests which, moreover, included numerous exotic plants. The authors assess the impact of highly disturbing logging operations and, based on the results of the comparisons, are very pessimistic about the possibility of maintaining species richness in logged forests. Nevertheless, the results indicate that the situation is not beyond hope and an eradication program specifically tailored to this kind of forest is proposed if exploitation will stop.

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Biological invasions are well known to contribute to biodiversity loss (Vitousek, 1988; Wilcove *et al*., 1998). Once introduced in a new area, the most suitable way to control alien invasive plants is eradication, while facilitating spontaneous indigenous regeneration in order to maintain species richness (Prach *et al*., 2001 a,b). This is the strategy adopted by forestry services. For many years they have been striving to associate wood production with the maintenance of species richness (e.g. Work *et al*., 2003). However, the idea that forests can serve multiple uses, including wood production and maintenance of high biodiversity level, is an untested hypothesis (Simberloff, 1999).

The endemic *Acacia heterophylla* Willd. forests of Réunion (Mascarene archipelago, Indian Ocean) offer a good opportunity to test this hypothesis with an experimental field approach. Although it belongs to one of the world biodiversity hotspots within the Malagasy region (Myers *et al*., 2000), the last 30% of intact virgin plant cover of Réunion are nowadays threatened by invasive alien plants (Strasberg *et al*., 2005; Baret *et al*., 2006). Since the first human settlement on Réunion in the 17$^{th}$ century, more than 2000 plant species have been introduced. Most of them are only cultivated as agricultural or ornamental in town and in small gardens but many species became subspontaneous and 62 species are now considered very invasive (Macdonald *et al*., 1991). The national forestry office tries to control these invasive alien plants, particularly *Rubus alceifolius* Poiret, the most widespread of these plants (Macdonald *et al*., 1991). For many years, at great expense, the forestry service has focused on eradicating this weed. The annual control expenses devoted solely to *Rubus* in 1983 (mainly manual control) were about 160 000 €, for an area of 345 ha (ONF, 1983).

In the last survey, 1 500 ha of exploited *Acacia* forests (logged since 1947, Miguet, 1957) were included in the last 5 500 ha of well preserved endemic *Acacia heterophylla* forests (Michon, 1998). *Rubus alceifolius* control expenses are particularly high in this type of habitat (particularly the exploited part), which is currently highly invaded (Strasberg *et al*., 2005). As exploited *A. heterophylla* forests are located on the border of the last natural 4 000 ha of preserved virgin forest, it is essential to control this invasive plant in exploited areas to keep it from spreading further and endangering the natural remnant forest patches. This has been the goal of the forestry services for more than 15 years (see review in Hivert, 2003). In 1990, a grey report estimated expenses linked to manual and chemical *R. alceifolius* control in this unique forest at 2 240 €/ha (Parret, 1990). Despite this financial output, this alien plant continues to invade and threaten *A. heterophylla* forests.

In order to determine whether wood production and biodiversity maintenance are compatible, we need to better understand eradication methods implemented in exploited *A. heterophylla* forests and compare species richness within logged forests and similar natural habitats. The goal of this study was therefore to gain insight into why *Rubus alceifolius* (alien plant which requires sustained intensive and costly eradication programs) continues to flourish in exploited *A. heterophylla* forests and, secondly, to determine whether species richness is maintained in these forests. The following questions were thus addressed: (1) What is the reason for new *R. alceifolius* infestations after eradication? (2) Do the growth ability and seed germination rate of *R. alceifolius* explain its invasiveness? and (3) What are the species richness differences between exploited and natural *A. heterophylla* forests?

In order to answer these questions, we focused our study on gaining insight into why only a single total cut (the main method used against *R. alceifolius*) of the invasive plant for eradication is not sufficient. We thus first aimed to confirm Miguet's hypothesis (1980), who considered that *R. alceifolius* invasion resulted from the growth of numerous seedlings after patches eradication. We also compared *R. alceifolius* and *A. heterophylla* growth. The growth and seed germination rates of both *Rubus* species (*R. alceifolius* and *R. apetalus* var. *apetalus*, an indigenous congener) were also compared. In order to assess the maintenance of species richness in exploited forests (for wood production), we also compared plant diversity between a logged *A. heterophylla* forest and a similar natural habitat.

The answers to these questions could help to orient eradication schemes in endangered endemic *Acacia heterophylla* forests and indicate whether or not wood production is compatible with species richness maintenance in forests.

# MATERIAL AND METHODS

## STUDY SITE

This study was carried out in Réunion (2 512 km$^2$), a volcanic island located in the southwestern Indian Ocean region (21°06'S, 55°32'E). Measurements were carried out at Bélouve (889 ha), at 1 500 m of elevation, with abundant precipitation (3 346 mm.year$^{-1}$) and with a mean annual temperature of 13.6°C. This locality was totally covered by *Acacia heterophylla* forest before human settlement in the 17$^{th}$ century. This habitat type includes a natural plant association dominated by *A. heterophylla* (an endemic species) associated with different endemic trees, ferns and orchids (consisting of 96 flowering plant species, including 41 endemic species, Strasberg *et al.*, 2005)

## STUDY SPECIES

*Acacia heterophylla* Willd.– This endemic species is taxonomically close to another phyllodinous species, *Acacia koa* A. Gray, endemic to Hawaii, and heterophyllous species do not occur on continents except Australia where they arose (Pedley, 1975; Coulaud *et al.*, 1995). In Réunion, this endemic tree grows (in pure or mixed stands) in a vast forest surrounding the island between 1 400 and 1 800 m of elevation, excluding areas where rainfall is heavy (more than 6 m precipitation per year). Before human settlement in the 17$^{th}$ century, this habitat area was estimated at 8 000 ha. Currently, 5 500 ha have been preserved, but used for its very good lumber (Miguet, 1980). This area includes 1 500 ha of regularly exploited *Acacia* forest (Michon, 1998). Cadet (1977) suggested that this forest is the result of bush burning. Seeds do not germinate under dense cover but numerous seedlings are observed after clearing or fire. Timber extraction by forestry services shows a total cut of *A. heterophylla* trees (which form a large part of the canopy). The studied plot was cleared in November 1998. Only tree ferns (*Cyathea glauca*, which is a protected species endemic to Réunion; ≈ 0.4 individuals.m$^{-2}$) had been preserved by foresters. They were not included in our analysis. Only new species that appeared after clearing were analysed.

*Rubus alceifolius* Poir. (Rosaceae).– This giant bramble (see Baret *et al.*, 2003) thrives in a moist sunny environment (forest edge, gaps, unploughed land, etc., Baret *et al.*, 2005a; Baret & Strasberg, 2005). Native to Southeast Asia, this species was introduced into the Mascarene Islands around 1850 (Cordemoy, 1895). Thereafter it proliferated on the eastern and southeastern coasts, where rainfall is the heaviest, from sea level up to 1 700 m a.s.l., whereas it is only found at 500 m a.s.l. and above in gullies along the western coast. Midway between a bush and a liana (Baret *et al.*, 2003a), this plant produces numerous fruits and seeds in the lowlands but grows only vegetatively above 1 100 m a.s.l. (Baret *et al.*, 2003b, 2004).

*Rubus apetalus* var. *apetalus* Poir. (Friedmann, 1997).– This is an indigenous taxon of Réunion, having the same life form of *R. alceifolius* but it is not very common. It grows in hygrophilous clearings, high thickets from 1 000 to 1 500 m a.s.l. This plant is also present in Madagascar and mountainous parts of East Africa.

## *R. ALCEIFOLIUS* ERADICATION METHODS

We focused our study on gaining insight into why only a single total cut of the invasive plant for eradication is not sufficient. We thus first aimed to test Miguet's hypothesis (1980), who considered that *R. alceifolius* invasions resulted everywhere from the germination of numerous seedlings after patches eradication. We also compared *R. alceifolius* and *A. heterophylla* and *R. alceifolius* and *R. apetalus* var. *apetalus* growth. The seed germination rates of both *Rubus* species were also compared. In order to assess the maintenance of species richness in exploited forests (for wood production), we compared plant species diversity between a logged *A. heterophylla* forest and a similar natural habitat.

## ORIGIN OF *RUBUS ALCEIFOLIUS* INFESTATION

*Rubus alceifolius* colonization could occur *via* seedlings, sprouts, terrestrial layering and cuttings (Baret *et al.*, 2003a; Baret *et al.*, 2005b). First, the reproductive modes used by *R. alceifolius* individuals (n=32) were randomly characterized within a 100-m$^2$ quadrat. When unable to determine the reproductive mode (individuals too small or damaged), we classified it as undetermined. Secondly, 16 random soil samples (10 x 10 cm x 5 cm deep) were collected in order to assess the potential seed bank at Bélouve. Most viable seeds are known to accumulate in this 5 cm deep layer (Leck *et al.*, 1989). *Rubus* seed bank was studied with a high efficiency in lowland forest following this protocol (Baret *et al.*, 2004). Eight samples were collected under a dense stand of *Rubus* and eight others in exploited *A. heterophylla* plots. Soil samples were mixed with a dispersant (Tween 80), passed through a sieve system with three stacked sieves (2, 1 and 0.5 mm mesh) and dried with a hairdryer before the seeds were counted.

These results will give an idea of the *Rubus alceifolius* seed bank and propagation mode that prevail in exploited *A. heterophylla* forests.

## *R. ALCEIFOLIUS* GROWTH CAPACITY AND SEED GERMINATION RATE

The growth of *R. alceifolius* and *A. heterophylla* was compared after the total cut of the exploited forest. *R. alceifolius* (n=32 individuals) and *A. heterophylla* (n=22 individuals) growth (stem length and basal diameter) was measured in the same 100-m$^2$ quadrat as described earlier. These results will give an idea of the growth ability of *Rubus alceifolius* that enables it to colonize and invade *Acacia heterophylla* forest.

The growth and seed germination rates of *R. alceifolius* and *R. apetalus* var. *apetalus* were compared. An effective way to identify mechanisms of invasive plant success is by comparing closely related invasive and non-invasive congeners that overlap the range and share morphological and life-history traits (Mack, 1996).

We compared *R. alceifolius* (alien invasive bramble) and *R. apetalus* var. *apetalus* (indigenous non invasive bramble) growth patterns by placing 45 cuttings of both species (15 at three different sites) under luminous 25-year-old exploited *Acacia* forest (500 stems.ha$^{-1}$). This experiment was first set up in November 2000. As only one cutting developed, the same experiment was renewed in February 2001. Note that the first experiment (November 2000) was conducted during the dry season when solar radiation was high and rain very low at the beginning of the experiment.

Seed germination rates of both indigenous and exotic *Rubus* plants were measured in July 2001. *R. apetalus* var. *apetalus* seeds were harvested in Bélouve in February 2001. As *R. alceifolius* does not fruit in the highlands (see Baret *et al*., 2004), we harvested its seeds in the lowlands (Grand-Brûlé, 50 m a.s.l.) on 15 March 2001. Seedling trays were randomly placed within an exploited 25-year-old *A. heterophylla* forest in the centre of three small gaps (around 25m$^2$). As seeds of *Rubus* species are known for their thick tegument and high dormancy (Marks, 1983), most seeds were first scarified using Amsellem's procedure (2000). This protocol involved plunging the seeds into 95% sulphuric acid during 45 mn before sowing. We sowed the two *Rubus* species (the indigenous *vs*. the exotic) seeds in different trays (in the three gaps), consisting of several pots (five seeds in each one). For each species, 80 scarified seeds (16 pots) and 20 other non-scarified (four control pots) were placed in the different gaps. To limit exchanges with natural sites, each tray was covered with a transparent perforated plastic sheet (i.e. lighting and water conditions were similar to those of the site). No non-scarified seeds germinated. These seeds were thus not used for calculating the seeds germination rates. As low temperatures could inhibit seedling growth in July 2001 (winter season), a similar experiment was performed in summer (January 2002).

### Species richness

To assess the impact of sylvicultural cutting on plant recolonization, flora surveys (identification of all species individuals > 5 cm high, except epiphytes) were conducted in both exploited and natural (control) forests. To determine the regeneration efficiency of different species after sylvicultural cutting (October 1998), numbers and heights (distinguishing four distinct layers: 5-25 cm, 25-100 cm, > 100 cm and > 400 cm) of individuals present in four 100-m$^2$ quadrats were recorded at different times (March and June 1999, March 2001; respectively 4, 8 and 28 months after plot clearing). The forestry service conducted chemical control operations to limit invasions. According to these agents, one of the four 100-m$^2$ quadrats (studied before to determine the *R. alceifolius* mode and compare its growth ability with that of *A. heterophylla*) where *Rubus alceifolius* was present at the beginning of the treatment, had not been controlled. New surveys were also conducted in August 2002 (45 months after clearing). At the same time, other flora surveys were undertaken in the nearest natural *A. heterophylla* forest. Four 100-m$^2$ plots (control) were delineated in this natural forest. The canopy was higher than in exploited plots, i.e. a supplementary layer (> 4 m) was observed. In these control plots, some trees reached 15-20 m height.

## RESULTS

### Origin of *Rubus alceifolius* infestation

Field observations showed that *Rubus alceifolius* grew mainly from cuttings (62.5%). The reproduction mode of some other individuals could not be determined because they were too small. We were unable to determine whether they grew from microcuttings or seedlings.

The seed bank study revealed that no *R. alceifolius* seed was present in the 16 soil samples under the *Rubus* storey or under exploited *A. heterophylla* stands.

### *R. alceifolius* growth capacity and seed germination

In our comparison of growth in *R. alceifolius* and *A. heterophylla*, differences in mean stem lengths were 1.93 greater for *R. alceifolius* (23.4 ± 3.4 cm) than for *A. heterophylla* individuals (12.1 ± 1.9 cm) 4 months after plot clearing. Differences in mean stem lengths were increasingly greater over time (mean length of 49.8 cm for *R. alceifolius* 8 months after plot clearing vs. 29.9 cm for *A. heterophylla*) (Fig. 1).

In our comparison of growth and seed germination in *R. alceifolius* and *R. apetalus* var. *apetalus*, 3 months after cutting plantations of 45 *R. alceifolius* and 45 *R. apetalus* cuttings in November 2000, only one *R. alceifolius* plant had developed (reaching 78 cm long and having a basal diameter of 5.3 mm in August 2002, Fig.2). All buds present along other cuttings had been totally desiccated by the sun. The cuttings had not withstood the dry season very well, particularly late in this study year. A new similar experiment conducted in February 2001 (during the rainy season) showed that 11 *R. alceifolius* cuttings (reaching a mean 912 cm in length and having a mean basal diameter of 6.7 mm in August 2002, where only five individuals had survived, see Fig. 2) had begun growing versus only one *R. apetalus* var. *apetalus* individual (observed only 3 months after the beginning of the experiment and having, at this date, a length of 4 cm, but it died thereafter). Concerning the seed germination rates, 3.75% (9 seeds from 240 sowed) of *R. alceifolius* seeds had emerged in July 2001 (winter season). Only one *R. apetalus* seedling (of 240 planted) was observed (0.83%). No seedlings of either species were observed during a similar experiment repeated in January 2003 (summer).

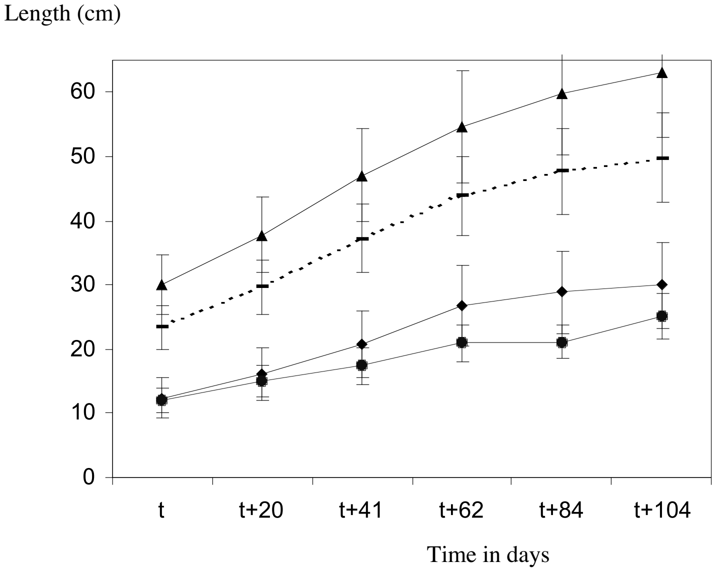


Figure 1. — Mean lengths of stems (± SE) of *Rubus alceifolius* (in relation to its reproductive mode) and *Acacia heterophylla* (seedlings only) individuals present in a 100-$m^2$ regeneration plot. t corresponds to the beginning of the observations, 4 months after plot clearing, and t+104 to 8 months after plot clearing (measurements were performed every 3 weeks). Triangles: *R. alceifolius* cuttings; -: all *R. alceifolius* individuals; diamonds: indeterminate mode of *R. alceifolius* individuals; circles: *A. heterophylla* individuals.

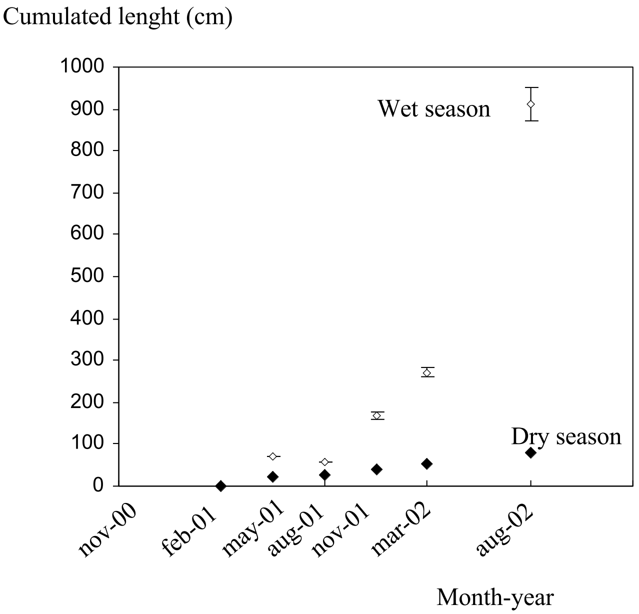


Figure 2. — Cumulated lengths of *Rubus alceifolius* stems were determined from cuttings under a 25-year old *Acacia heterophylla* storey. Black diamonds: experiment set up in November 2000 (dry season); white diamonds: experiment set up in February 2001 (wet season). 45 cuttings were planted at the beginning of both experiments for both *Rubus* species. No *R. apetalus* growth over time.

## FLORISTIC DIVERSITY IN EXPLOITED AND NATURAL *A. HETEROPHYLLA* FORESTS

*Exploited forest*

The number of alien plants (from a mean 15.8 individuals per 100 $m^2$, 4 months after plot clearing to 51.8 individuals 28 months after) and species richness (from a mean 3.50 different species 4 months after plot clearing to 10.3 species 28 months after) increased significantly over time, although the indigenous number significantly decreased (from a mean 74.3 individuals to 19.5, respectively, for the same months, see Table I). The measures completed 45 months after clearing, confirmed the progression in the number of exotic (124 individuals observed) and indigenous (8 individuals) plants but there was a change in the species richness (only 4 different species were present). The species richness and the number of indigenous remained significantly higher in the natural forest (see Table I).

TABLE I.

*Indigenous versus alien plant number and species richness (means ± SE) measured in natural and exploited* A. heterophylla *forests on four 100-m² plots during 28 months (except 45 months after clearing, when only one 100-m² plot was monitored). The percentages of indigenous individual numbers and species are also expressed*

| | Indigenous number (/ 100m²) | Alien number (/ 100m²) | Species richness (/ 100m²) | Indigenous individuals (%) | Indigenous species (%) |
|---|---|---|---|---|---|
| Natural | 161 ± 21.0 $^{a}$ | 11.5 ± 3.38 $^{a}$ | 20.3 ± 1.65 $^{a}$ | 93.3 | 88.9 |
| Clearing + 4 months | 74.3 ± 10.5 $^{b}$ | 15.8 ± 11.15 $^{a, c}$ | 3.50 ± 0.29 $^{b}$ | 82.5 | 50.0 |
| Clearing + 8 months | 75.8 ± 7.11 $^{b}$ | 24.8 ± 5.20 $^{a, c}$ | 6.75 ± 1.11 $^{c}$ | 75.4 | 51.9 |
| Clearing + 28 months | 19.5 ± 2.53 $^{c}$ | 51.8 ± 14.0 $^{b, c}$ | 10.3 ± 1.49 $^{c}$ | 27.1 | 46.3 |
| Clearing + 45 months | 8 | 124 | 4 | 6.1 | 50.0 |

For these variables, a change in letter means that the values were significantly different at the 5% level according to a Mann–Whitney test (Statistix 7, 1998).

Four months after plot clearing (except for *Cyathea glauca,* which was preserved during clearing), the most abundant species observed was *A. heterophylla*, but it was only present in the 5-25 cm layer. Few exotic individuals appeared, i.e. *R. alceifolius*, *Juncus effusus*, *Solanum mauritianum* and *Fuchsia* x *exoniensis*, but they were less abundant than indigenous individuals (Table II). Eight months after clearing, indigenous individuals were still more abundant than exotics in the 5-25 cm layer. In the higher layers, exotic species appeared and were more abundant than indigenous species. Sixteen months after plot clearing, exotic plants were more abundant than indigenous plants in all layers (Table II). Although exotic individuals were more abundant, similar trends were noted within a 100-$m^2$ plot at the same time after clearing. Indigenous species were more abundant 4 and 8 months after plot clearing within the 5-25 cm layer. Nevertheless, only two exotic species were recorded at these dates and one (*R. alceifolius*) was already present 4 months after clearing in the 25-100 cm layer. A floristic survey conducted 45 months after plot clearing showed that *Rubus alceifolius* formed a stand with only eight indigenous plants: seven *A. heterophylla* and one *Dombeya ficulnea* had persisted (mainly in the layer above 100 cm high).

## Table II

*Number of plants observed in two 400-m² natural and exploited (respectively 4, 8, 28 and 45 months after clearing) forest plots according to different strata: S1 or 5-25 cm strata, S2 or 25-100 cm strata, S3 or > 100 cm strata, S4 or > 400 cm strata (only present in natural forests). Alien plant species are represented in bold.*

| | EXPLOITED | | | | | | | | | | | | NATURAL | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | +4 | | | +8 | | | +28 | | | +45 (* 4) | | | | | | |
| | S1 | S2 | S3 | S1 | S2 | S3 | S1 | S2 | S3 | S1 | S2 | S3 | S1 | S2 | S3 | S4 |
| *Acacia heterophylla* | 292 | | | 28 | 11 | | 16 | 37 | 15 | | 4 | 24 | | | 9 | 4 |
| *Acanthophoenix rubra* | | | | | | | | | | | | | | 5 | | |
| ***Ageratina riparia*** | | | | | | | 1 | | | | | | | | | |
| *Antirhea borbonica* | | | | | | | | | | | | | | | 13 | 1 |
| *Aphloia theiformis* | | | | | | | | | | | | | 10 | | 7 | 2 |
| *Asplenium attenuatum* | | | | | | | | | | | | | 75 | | | |
| *Asplenium lineatum* | | | | | | | | | | | | | 45 | | | |
| *Astellia hemichrysa* | | | | | | | | | | | | | 185 | 10 | | |
| ***Begonia cucullata*** | | | | 1 | | | | 5 | | | | | | | | |
| *Berteria rufa* | | | | | | | | | | | | | 10 | | 10 | |
| *Blotiella pubescens* | 4 | | | 7 | | | | | | | | | 5 | 30 | 6 | |
| *Chassalia corallioides* | | | | | | | | | | | | | | 5 | | |
| *Chassalia gaertneroides* | | | | | | | | | | | | | | 30 | 45 | |
| *Claoxylon glandulosum* | | | | | | | | | | | | | | | 6 | 1 |
| *Clematis mauritiana* | | | | | | | | | | | | | | | 5 | |
| *Cyathea glauca* | | | 14 | | | 14 | | | 14 | | | | | 10 | 16 | 14 |
| *Dombeya ficulnea* | | | | | | | | 1 | | | | 4 | | | | |
| *Dombeya pilosa* | | | | | | | | | | | | | | | 1 | 1 |
| *Doratoxylon apetalum* | | | | | | | | | | | | | 5 | | | |
| *Embelia angustifolia* | | | | | | | | | | | | | 5 | | | |
| *Euodia obtusifolia* | | | | | | | | | | | | | 5 | | | |
| *Forgesia racemosa* | | | | | | | | | | | | | | | 1 | |
| ***Fuchsia magelanica*** | | | | | | | | | | | | | 5 | | 10 | |
| ***Fuchsia x exoniensis*** | 2 | | | 2 | 2 | | | 3 | | | | | | | | |
| *Gaertnera vaginata* | | | | | | | | | | | | | 5 | | 17 | 1 |
| *Hubertia ambavilla* | | | | 1 | | | | 1 | | | | | | | | |
| *Humbertacalia tomentosa* | | | | | | | | | | | | | 5 | 10 | 5 | |
| *Hypericum lanceolatum* | | | | | | | | | | | | | | 5 | 1 | 1 |
| ***Juncus effusus*** | 6 | | | 4 | 8 | | | 55 | 12 | | | | | | | |
| *Monimia rotundifolia* | | | | | | | | 1 | | | | | | | 9 | 8 |
| *Nuxia verticillata* | 1 | | | | 1 | | | | | | | | | | 13 | 1 |
| *Ocotea obtusata* | | | | | | | | | | | | | | 5 | | |
| *Oleandra distensa* | | | | | | | | | | | | | 5 | | | |
| *Psiadia anchusifolia* | | | | 3 | | | | 4 | 2 | | | | 5 | | | |
| ***Rubus alceifolius*** | 46 | 2 | | 34 | 27 | 4 | 31 | 38 | 3 | 128 | 176 | 180 | 5 | 5 | 15 | |
| ***Solanum mauritianum*** | 6 | 1 | | 15 | 2 | | 9 | 11 | 12 | | 4 | 8 | | | 6 | 1 |
| *Stoebe passerinoides* | | | | | | | | 1 | | | | | | | | |
| *Weinmannia tinctoria* | | | | | | | | | | | | | | | 4 | 4 |

As the forestry service conducted chemical control operations to limit invasiveness, only one 100-m² quadrat was untreated 28 months after plot clearing. Therefore, in the above table, we multiplied our results obtained in exploited forests (45 months after plot clearing) by four in order to make a valid comparison of areas between years and forest types.

*Natural forest*

The species richness was 20.3 species per $100m^2$ (Table I) and most individuals (93.3%) and species (88.9%) were indigenous. The > 400 cm high layer was occupied by 38 individuals, predominated by *Cyathea glauca* and *Monimia rotundifolia*. The > 100 cm high layer was occupied by 159 individuals. The most abundant were two different endemic Rubiaceae species, i.e. *Chassalia gaertneroides* and *Gaertnera vaginata*. *C. glauca*, *Antirhea borbonica* and *Nuxia verticillata* were also abundant (see Table II). *Acacia heterophylla* was just represented by nine individuals.

110 and 365 individuals, mainly indigenous, formed the 25-100 and 5-25 cm layers, respectively. *Acacia heterophylla* was abundant in these two layers (10 and 185 individuals, respectively). *Chassalia gaertneroides* and three ferns, i.e. *Blotiella pubescens*, *Asplenium attenuatum* and *Asplenium lineatum,* were also abundant in these two lower layers (Table II).

Only three alien plant species were observed in this natural forest, i.e. *Rubus alceifolius*, *Fuchsia magellanica* and *Solanum mauritianum,* and in small numbers (Table II).

## DISCUSSION

Are wood production and species richness maintenance compatible? In our study we tested this unproven hypothesis (Simberloff, 1999) through comparisons of logged and natural endemic *Acacia heterophylla* forests. The current management of logged forest was also quantified in the field through *R. alceifolius* (the most widespread alien plant in Réunion) presence, growth and seed germination.

### Invasion mechanisms

Although *Rubus alceifolius* is known to be disseminated by frugivorous birds (Mandon-Dalger, 2002), it is likely that this dissemination strategy certainly does not apply to long-distance invasion. Although Baret *et al*. (2004) have shown that *R. alceifolius* fruits abundantly in lowland areas (below 1100 m a.s.l.), no seed was observed in the soil at our study site (1500 m) and usually above 1100 m (Baret *et al*., 2004). Our results are thus out of line with those obtained by the forester Miguet (1980), who considered that *R. alceifolius* proliferation was linked to abundant seed dissemination by frugivorous birds and observed numerous seedlings after clearing. Our first results were confirmed when we observed, after clearing, that all identified individuals had grown from cuttings derived from individuals present prior to the clearing operation. Indeed, the clearing method used by the forestry service was rapid and numerous cuttings were left on the ground after a total cut of the bramble cover (pers. obs.). Cuttings could thus develop *via* sprouts and successive apical rooting (terrestrial layering), easily and rapidly forming (around 2.5 years) large patches that could grow readily under luminous *A. heterophylla* exploited forest (see Baret *et al*., 2003a, for a *R. alceifolius* development analysis). To our knowledge, this is the first time that a quantitative scientific study has been undertaken in the field to assess whether eradication methods can favour alien plant invasiveness (case of *R. alceifolius* in *A. heterophylla* exploited forest). Therefore, as Simberloff (1999) suggested, we highlight here the importance of scientifically assessing invasive plant control methods in order to approve them or not. Invasive alien plant eradication is very expensive and thus needs to be well adapted to totally eradicate the invasive plants and not favour their regrowth. Before eradication, it is thus essential to investigate the biology and ecology of the invasive plant in order to gain further insight into its invasive strategy.

### *R. alceifolius* growth capacity and seed germination rate

*Comparison of growth with* Acacia heterophylla

*R. alceifolius* rapidly abounded after the trees were cut (≈ 2 $individuals.m^{-2}$) only 4 months after clearing. *Acacia heterophylla* seedlings also rapidly appeared (around 0.7 $individuals.m^{-2}$, 4 months after clearing). However, *R. alceifolius*, which seemed to be more competitive, quickly colonized the plot and formed a monospecific stand (16-45 months after clearing, see Table II). Four months after clearing, mean *R. alceifolius* stem lengths were around twofold greater than noted for *A. heterophylla*. This difference steadily increased during the study. We confirmed here a specific trait of invasive species, whereby exotic species have a higher growth rate than indigenous species (Grotkopp *et al*., 2002). Better competitivity and capacity to withstand disturbances as compared to indigenous species are known features (Lonsdale, 1999). Nevertheless, the greater growth rate of *R. alceifolius* relative to *A. heterophylla* could be related to its life form. Baret *et al*. (2003a) pointed out that the life form of *R. alceifolius* is midway between a bush and a liana, and indicated that it shows a specific preference for both open and half-open areas. Thus a similar life form (characterized by *Rubus apetalus* var. *apetalus*, a similar indigenous species) could confirm whether *Rubus alceifolius* is really more competitive than indigenous plant (see Mack, 1996).

*Comparison of growth and seed germination rate with indigenous* Rubus *species*

The results showed that cutting survival was higher for exotic *Rubus* species than for indigenous species (11.1% vs. 0% 1 year after the beginning of the experiment). We could not compare growth as no *R. apetalus* var. *apetalus* (indigenous) survived over time. Concerning the seed germination rate of both *Rubus* species (seeds from a lowland area for *R. alceifolius*), our results showed a higher rate of germination for *R. alceifolius* as compared to *R. apetalus* var. *apetalus* (3.75% and 0.83%, respectively) — this difference was minor, non-significant and seasonally dependent (seedlings observed only in winter, none in summer). Thus, even though few seeds reached highland areas, the germination potential is poor and also seasonally dependent. Some seeds transported in sand by trucks (road building for timber extraction) certainly enabled *Rubus alceifolius* to colonize the highlands. Once established, *R. alceifolius* could grow rapidly, while not hindering regenerating indigenous species, but gradually excluding competing individuals by developing large stands. Baret *et al.* (2004) showed that sprouts and new axes formed by apical rooting also grow rapidly. This development strategy (vegetative propagation) could enable *R. alceifolius* plants to rapidly invade an environment. Indeed, in this species, cuttings showed greater development than seedlings, forming large patches within only 2.5 years after total clearing. A rapid juvenile period is considered to be typical of invasive species (Rejmánek & Reichard, 2001).

We measured the high vegetative capacities of *R. alceifolius* and gained further insight into the incapacities of the forestry service to effectively control this species without a scientific approach.

COMPARISON OF SPECIES RICHNESS IN NATURAL AND LOGGED *A. HETEROPHYLLA* FORESTS

A comparison of species richness in natural and exploited *Acacia heterophylla* forests showed that the floristic diversity was higher in the natural *A. heterophylla* forest (31 plant species per 400 $m^2$) than in the exploited forest (12 species per 400 $m^2$ 16 months after plot clearing, Table II). Even though the species area curves appeared to increase progressively in exploited forests (Fig. 3), the subsequent plant diversity of the forest was partially decreased by invasive plants. Half (six) of the species observed in exploited forests were exotic, as compared to only three alien plant species observed in natural forests. The use of non-efficient eradication methods is really at risk because it could lead to high costs for controlling alien invasive plants, while it favours propagation of invasive plants in the nearest natural forest. Indeed, alien plant species observed are known to be very invasive and are amongst the 33 species capable of colonizing natural ecosystems (see MacDonald *et al*., 1991). Facilitating their development thus appears very threatening, particularly in an already endangered native forest. Our results are similar to those reported by Tilman *et al*. (1997), Lavorel *et al*. (1999), Symstad (2000), Dukes (2001), and sustain Elton's hypothesis (1958) that a diversified ecosystem is more resistant to alien plant invasiveness (see Fig. 3 for a species-area curve comparing a logged and a natural forest).

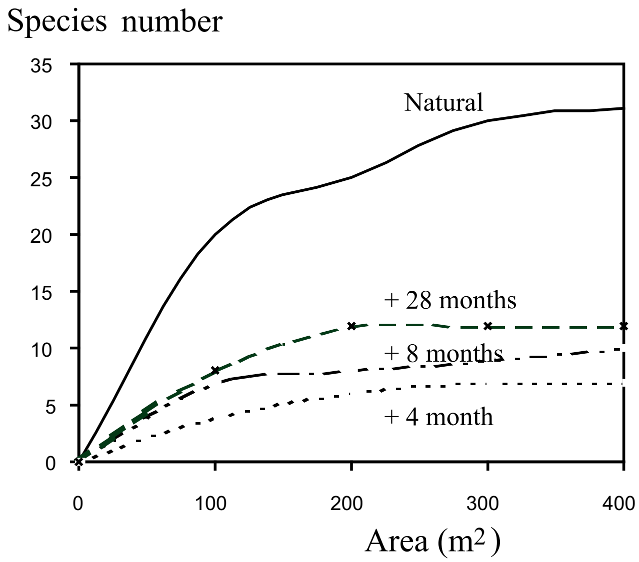


Figure 3. — Species - Area curves for a natural and an exploited *Acacia heterophylla* forests. For the exploited forest, the values were recorded 4, 8 and 28 months after plot clearing.

## Enhancing forest management practices

Following our results, the idea that forests can always serve multiple uses, including wood production and maintenance of high biodiversity level, is not realistic. Currently, the future of the last 5 500 ha of the endemic *A. heterophylla* forests in Réunion seems very gloomy. Although a 'back to nature' approach (see Gamborg & Larsen, 2003) could be the only way to maintain equivalent species richness in undisturbed and natural *A. heterophylla* forests, we suggest that an efficient eradication program of invasive plants (according to our results) could certainly enhance the number of indigenous species in logged forests.

Firstly, logging or clearing the plot would be more efficient if conducted during the dry season (September-October). At this moment, buds present on cuttings of *R. alceifolius* could be rapidly desiccated by only 2-3 days of sunshine (pers. obs.). To stall the growth of *R. alceifolius* cuttings, individuals could be uprooted and leaved on the tree. Apical *R. alceifolius* stems must be kept off the ground to avoid rooting (see Baret *et al.*, 2003a, for the location of this stem part). A new rapid intervention could be undertaken the next year. Thus, as this species cannot fruit in highland areas and no seed accumulate in the soil above 1 100 m a.s.l., *R. alceifolius* could be progressively eradicated at the Bélouve site (889 ha) and progressively thereafter in all exploited forests located in highlands of Réunion. Efficient eradication of alien invasive plants will facilitate spontaneous indigenous regeneration and maintenance. *Acacia heterophylla* forests and its associated biodiversity could be preserved. An adapted eradication program has already been organized and is currently being implemented by the forestry services in exploited *Acacia heterophylla* forests (see Hivert, 2003). A scientific species richness comparison needs to be done in the future (few years) in order to confirm or not the higher species richness. Nevertheless, future cuts of *A. heterophylla* trees represent a serious threat since a high disturbance level (such as timber extraction) within a plant community is known to increase invasion by alien plants (Horvitz *et al.*, 1998). Logging techniques need to be improved in the future in order to avoid facilitating colonization by alien invasive plants due to total canopy opening and vegetative multiplication of aliens.

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## REFERENCES

AMSELLEM, L. (2000). — *Comparaison entre aires d'origine et d'introduction de quelques traits biologiques chez* Rubus alceifolius *Poir. (Rosaceae), plante envahissante dans les îles de l'océan Indien.* PhD thesis, University of Montpellier II, Montpellier, France.

BARET, S., LE BOURGEOIS, T. & STRASBERG, D. (2005a). — Comment *Rubus alceifolius*, une espèce exotique envahissante, pourrait-elle progressivement coloniser la totalité d'une forêt tropicale humide? *Can. J. Bot.*, 83: 219-226.

BARET, S., MAURICE, S., LE BOURGEOIS, T. & STRASBERG, D. (2004). — Altitudinal variation in fertility and vegetative growth in the invasive plant *Rubus alceifolius* Poiret (Rosaceae), on Réunion island. *Plant Ecol*., 172: 265-273.

BARET, S., NICOLINI, E., HUMEAU, L., LE BOURGEOIS, T. & STRASBERG, D. (2003b). — Use of architectural and morphometric analysis to predict the flowering pattern of the invasive *Rubus* on Réunion island. *Can. J. Bot*., 81: 1293–1301.

BARET, S., NICOLINI, E., LE BOURGEOIS, T. & STRASBERG, D. (2003a). — Development patterns of the invasive bramble (*Rubus alceifolius* Poiret, Rosaceae) in Réunion Island: an architectural and morphometric analysis. *Ann. Bot. (London)*, 91: 3-48.

BARET, S., RADJASSEGARANE, S., LE BOURGEOIS, T. & STRASBERG, D. (2005b). — Does the growth rate of different reproductive modes of an introduced plant cause invasiveness? *Int. J. Bot.*, 1: 5-11.

BARET, S., ROUGET, M., RICHARDSON, D.M., LAVERGNE, C., EGOH, B., DUPONT, J. & STRASBERG, D. (2006). — Current distribution and potential extent of the most invasive alien plant species on La Réunion (Indian Ocean, Mascarene islands). *Austral Ecol.*, 31: 747-758.

BARET, S. & STRASBERG, D. (2005). — The effects of opening trails on exotic plant invasion in protected areas on La Réunion island (Mascarene archipelago, Indian Ocean). *Rev. Ecol. (Terre Vie)*, 60: 325-332.

CADET, T. (1977). — *La végétation de l'île de La Réunion*. PhD thesis, University of Aix-Marseille, Aix-Marseille, France.

COULAUD, J., BROWN, S.C. & SILJAK-YAKOVLEV, S. (1995). — First cytogenic investigation in populations of *Acacia heterophylla*, endemic from La Réunion Island, with reference to *A. melanoxylon*. *Ann. Bot. (London)*, 75: 95-100.

DUKES, J.S. (2001). — Biodiversity and invisibility in grassland microcosms. *Oecologia*, 126: 563-568.

ELTON, C.S. (1958). — *The ecology of invasions by animals and plants*. Methuen, London.

FRIEDMANN, F. (1997). — Rosaceae. Pp. 1-11, *in*: *Flore des Mascareignes - La Réunion, Maurice, Rodrigues*. ORSTOM, Paris, France.

GAMBORG, C. & LARSEN, J.B. (2003). — 'Back to nature'– a sustainable future for forestry? *For. Ecol. Manage*., 179: 559-571.

GROTKOPP, E., REJMÁNEK, M.& ROST, T.L. (2002). — Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pines (*Pinus*) species. *Am. Nat*., 159: 396-419.

HIVERT, J. (2003). — *Plantes exotiques envahissantes: état des méthodes de lutte mises en œuvre par l'Office National des Forêts à La Réunion*. ONF, Réunion, France.

HORVITZ, C., PASCARELLA, J., MCMANN, S., FREEDMAN, A. & HOFSETTER, R.H. (1998). — Functional roles of invasive non-indigenous plants in hurricane-affected subtropical hardwood. *Ecol. Appl*., 8: 947-974.

CORDEMOY, E.J. DE (1895). — *Flore de l'île de La Réunion (Phanérogames, Cryptogames vasculaires, Muscinées) avec l'indication des propriétés économiques & industrielles des plantes*. Librairie des sciences naturelles, Paul Klincksieck, Paris.

LAVOREL, S., PRIEUR-RICHARD, A.H. & GRIGULIS, K. (1999). — Invasibility and diversity of plant communities: from patterns to processes. *Diversity Distributions*, 5: 41-49.

LECK, M.A., PARKER, V.T. & SIMPSON, R.L. (1989). — *Ecology of soil seed banks*. Academic press, Harcourt Brace Jovanovich, Publishers.

LONSDALE, W.M. (1999). — Global patterns of plant invasions and the concept of invisibility. *Ecology*, 80: 1522-1536.

MACDONALD, I.A.W., THÉBAUD, C., STRAHM, W.A. & STRASBERG, D. (1991). — Effects of alien plant invasions on native vegetation remnants on La Réunion (Mascarene Islands, Indian Ocean). *Envir. Cons*., 18: 51-61.

MACK, R.N. (1996). — Predicting the identity and fate of plant invaders: emergence and emerging approaches. *Biol. Cons.*, 78: 107-121.

MANDON-DALGER, I. (2002). — *Sélection de l'habitat et dynamique d'invasion d'un oiseau introduit, le cas du Bulbul orphée à la Réunion*. Ph.D. Dissertation, Université de Rennes 1, France.

MARKS, P.L. (1983). — On the origin of field plants of the northeastern United States. *Am. Nat*., 122: 210-228.

MICHON, R. (1998). — Tamarin des hauts et tamarinaies à la Réunion: vers la gestion durable d'une espèce unique au monde. *ONF-Bull. Tech*., 36: 79-89.

MIGUET, J.M., (1957). — Mise en valeur et régénération de la forêt de tamarins des hauts en zone d'altitude. La forêt de Bélouve à la Réunion. *Rev. For. Fr.*, 8: 285-310.

MIGUET, J.M.(1980). — Régénération et reconstitution de forêts naturelles à l'île de la Réunion. *Rev. Ecol. (Terre Vie)*, 34: 3-22.

MYERS, J.H., SIMBERLOFF, D., KURIS, A.M.& CAREY, J.R. (2000). — Eradication revisited: dealing with exotic species. *TREE*, 15: 316-320.

PARRET, J. (1990). — *Lutte contre la vigne marronne en forêt de Bélouve*. Rapport d'utilisation de produits phytocides. ONF, Réunion, France.

PEDLEY, L. (1975). — Revision of the extra-Australian species of *Acacia* subg. *Heterophyllum*. *Contributions from the Queensland Herbarium*, 18: 1-24.

PRACH, K., BARTHA, S., JOYCE, C.B., PYŠEK, P., VAN DIGGELEN, R. & WIEGLEB, G. (2001a). — The role of spontaneous vegetation succession in ecosystem restoration: a perspective. *Appl. Veget. Sc.*, 4: 111-114.

PRACH, K., PYŠEK, P. & BASTL, M. (2001b). — Spontaneous vegetation succession in human-disturbed habitats: a pattern across seres. *Appl. Veget. Sc.*, 4: 83-88.

REJMÁNEK, M. & REICHARD, S. (2001). — Predicting invaders. *TREE*, 16: 545-546.

SIMBERLOFF, D. (1999). — The role of science in the preservation of forest biodiversity. *For. Ecol. Manage*., 115: 101-111.

STATISTIX (1998). — *Analytic software*. Borland International, Tallahassee, Tenn.

STRASBERG, D., ROUGET, M., RICHARDSON, D.M., BARET, S., DUPONT, J. & COWLING, R.M. (2005). — An assessment of habitat diversity, transformation and threats to biodiversity on Réunion Island (Mascarene Islands, Indian Ocean) as a basis for conservation planning. *Biodiv. Cons.*, 14: 3015-3032.

SYMSTAD, A.J. (2000). — A test of the effects of functional group richness and composition on grassland invasibility. *Ecology*, 81: 99-109.

TILMAN, D., KNOPS, J., WEDIN, D., REICH, P., RITCHIE, M. & SIEMANN, E. (1997). — The influence of functional diversity and composition on ecosystem processes. *Science*, 277: 1300-1302.

VITOUSEK, P.M.(1988). — Diversity and biological invasions on oceanic islands. Pp. 181-189, *in*: E.O. Wilson & F.M.Peter (eds). *Biodiversity*. National Academy Press, Washington DC.

WILCOVE, D.S., ROTHSTEIN, D., DUBOW, J., PHILLIPS, A. & LOSOS, E. (1998). — Quantifying threats to imperilled species in the United States. *BioScience*, 48: 607-615.

WORK, T.T., SPENCE, J.R., VOLNEY, W.J.A., MORGANTINI, L.E., & INNESS, J.L. (2003). — Integrating biodiversity and forestry practices in western Canada. *For. Chron.*, 79: 906-916.