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CONTRIBUTION OF ACTINORHIZAL PLANTS TO TROPICAL SOIL PRODUCTIVITY AND REHABILITATION

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Summary—The contribution of actinorhizal plants to soil productivity and rehabilitation depends not only on properties encountered in a number of non-N_2-fixing trees but also on the input of fixed N_2 that is subsequently transferred to soil and ultimately to associated crops. The nitrogen-fixing potential of a number of actinorhizal plants (e.g. *Casuarina* sp. and *Alnus* sp.) is high but the amount of N_2 actually fixed in the field is often low because the expression of this potential is limited by unfavorable environmental conditions or improper management practices. Assessing the amount of fixed N_2 transferred to soil is difficult mainly because of the recycling of fixed N_2 except in open ecosystems. Many examples of successful introductions of actinorhizal plants into various systems of land management are given. To increase the input of fixed N_2 into ecosystems two strategies can be adopted: the first one is to use proper management practices; the second one is to improve the performances of the N_2-fixing system. Practically, in addition to optimizing actinorhizal fixation, it is recommended to develop the introduction of actinorhizal plants as soil improvers in a number of countries where they are not yet used, to domesticate hitherto neglected or overlooked actinorhizal plants, and to exploit their ability to contribute to the rehabilitation of wasted lands and possibly to the phytoremediation of polluted sites. © 1997 Elsevier Science Ltd

INTRODUCTION

Plants symbiotically associated with the N_2-fixing actinomycete *Frankia*, collectively called actinorhizal plants, belong to 24 genera distributed among eight plant families. Therefore, until recently, the impression was one of taxonomic unrelatedness (Bond, 1983), but recent molecular analyses suggest that actinorhizal plants are more closely related than usual morphologically based classification systems indicate (Swensen and Mullin, 1995). It must be noted that many closely related taxa do not bear actinorhizal nodules and there is no clear information on the molecular nature of barriers or common factors in actinorhizal symbiosis (Berry, 1994).

Native actinorhizal plants are not evenly distributed worldwide (Table 1). Whereas many species of actinorhizal plants are found in Australia, Asia, Europe, South and North America, Africa is particularly lacking in native actinorhizal plants, with the possible exception of several species of *Myrica* (Baker and Mullin, 1992).

This paper is an attempt to evaluate the current contribution of the best known actinorhizal plants to soil productivity and rehabilitation of wasted lands especially in tropical and mediterranean climates and to suggest the strategies that should be developed to increase significantly their potentialities in the near future. The most important actinorhizal plants belong to the *Alnus* genus and to the Casuarinaceae family. In the humid tropics they are *Casuarina cunninghamiana, C. equisetiffolia, C. junghuhniana, C. oligodon, Gymnostoma sumatrana*; in semi-arid and arid regions *Casuarina cristata, C. decaisneana, C. glauca* (irrigated), *C. cunninghamiana* (irrigated), *C. obesa* (irrigated); in tropical highlands *Alnus jorullensis/acuminata, A. nepalensis, A. glutinosa, Casuarina cunninghamiana, C. equisetifolia, C. junghuhniana* and in mediterranean regions *Alnus glutinosa, A. subcordata, Allocasuarina verticillata, Casuarina cunninghamiana, C. glauca.* In addition, a few tropical and temperate species belonging to the following genera will be considered here: *Coriaria, Elaeagnus, Hippophaë* and *Myrica.*

AMOUNT OF N_2 FIXED

The contribution of actinorhizal plants to soil productivity depends not only on properties found in a number of non-N_2-fixing trees (e.g. redistribution of nutrients through the soil profile, protection from erosion, improvement of soil physical conditions, shading and modification of the microclimate, weed suppressing effects) (Prinsley and Swift, 1986), but also on the input of fixed N_2 that is subsequently transferred to the soil and possibly to associated crops or non-fixing trees. Therefore it is

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Table 1. Distribution of representative genera of actinorhizal plants (after Baker and Mullin, 1992)

Family	Genus	Native from following regions[a]
Betulaceae	*Alnus*	NAm, SAm, Eur, NAs, SAs
Casuarinaceae	*Allocasuarina*	Aus
	Casuarina	Aus
	Gymnostoma	Aus
Coriariaceae	*Coriaria*	Aus, NAm, S Am, Eur
Datiscaceae	*Datisca*	NAm, SAs
Elaeagnaceae	*Elaeagnus*	NAs, NAm, Eur, SAs
	Hippophaë	Eur, NAs
	Shepherdia	NAm
Myricaceae	*Myrica*	SAf, NAm, SAm, Aus, SAs, NAs
	Comptonia	NAm
Rhamnaceae	*Adolphia*[b]	NAm
	Ceanothus	NAm
	Colletia	SAm
Rosaceae	*Cercocarpus*	NAm
	Dryas	NAm
	Purshia	NAm

[a] NAm = North America, SAm = South America, Eur = Europe, Aus = Australia and/or Oceania, SAf = southern Africa, NAs = northern Asia, SAs = southern Asia.

[b] Cruz-Cisneros and Valdes (1990).

essential to estimate the amount of N_2 fixed in each situation.

It must be noted here that a distinction has to be made between the N_2-fixing potential of a given N_2-fixing system and its actual N_2 fixation.

By N_2-fixing potential we designate the amount of N_2 fixed in a constraint-free environment. This ideal value could theoretically be determined by growing the system under the most favorable conditions. Such an evaluation has been attempted in the case of *Casuarina equisetifolia* by growing this actinorhizal plant inoculated with an effective *Frankia* strain in a soil with a low content of available N, proper addition of P, K and trace elements, careful irrigation and appropriate climatic conditions. The N_2-fixing potential of 2-year old *C. equisetifolia* was shown to be ca. 42·4 g N_2 fixed tree^{-1} y^{-1}, which would be 84·8 kg N_2 fixed ha^{-1} y^{-1} in a plantation of 2000 trees ha^{-1} (Dommergues, 1995). This is indeed a high N_2-fixing potential for a 2-year-old actinorhizal plant. A rough prediction of the N_2-fixing potential can be based on the assumption that the highest active nodule biomass observed reflects the N_2-fixing potential to a certain extent. Thus the following species could be considered as having a high N_2-fixing potential: *Alnus glutinosa* whose nodule biomass was estimated to be up to 454 kg ha^{-1} (Akkermans and Van Dijk, 1976) and *Alnus nepalensis* with 307 kg nodules ha^{-1} (Sharma and Ambasht, 1986). With the exception of *Casuarina equisetifolia* and some *Alnus* spp that have been shown to have a high N_2-fixing potential, data are still missing that would allow one to classify the different tropical actinorhizal plants according to their N_2-fixing potential.

A certain number of evaluations of the amount of N_2 actually fixed in the field by tropical actinorhizal plants have been published during the last 10 years. The most reliable are presented in Table 2. It appears that the actual N_2 fixation of *Casuarina equisetifolia* varies considerably irrespective of the mode of expression used: actual N_2 fixation expressed on an area basis ranges from 15 to 94 kg N_2 fixed ha^{-1} y^{-1}; actual N_2 fixation expressed per individual tree ranges from 6 to 47 g N_2 fixed tree^{-1} y^{-1}. Actual N_2 fixation of *Myrica faya* was found to be 18 kg ha^{-1} y^{-1}, a figure lower than expected since this small tree is known to be an aggressive colonizer. Generally the actual N_2 fixation appears to be lower—and even much lower—than usually assumed. It is low not only in species with a poor N_2-fixing potential but also in species with a high N_2-fixing potential whenever its expression is limited by unfavorable environmental conditions, such as climate and soil constraints, improper management techniques, absence of irrigation or fertiliza-

Table 2. Ndfa% (percentage of N derived from N_2 fixation) and actual nitrogen fixation (kg N_2 fixed ha^{-1} y^{-1} and g N_2 fixed tree^{-1} y^{-1}) in *Casuarina equisetifolia* and *Myrica faya* as assessed in the field

Species and country	Age (years)[b]	No. of trees ha^{-1}	Ndfa%	N_2 fixed (kg ha^{-1} y^{-1})	N_2 fixed (g tree^{-1}y^{-1})	Method and reference[c]
			Casuarina equisetifolia			
Senegal M[a]	13	2000		58	29	Bal. Dommergues (1963)
id.	6–38	1600		75	47	Bal. Mailly and Margolis (1992)
Senegal N[a]	3	2500	39	15	6	NA Mariotti *et al.* (1992)
id.	3	2500	33	15	6	Dif. Mariotti *et al.* (1992)
Puerto Rico	2 (M)	10000	48–55	66–77	7–8	Enr. Parrotta *et al.* (1994)
id.	2 (C)	5000	64–67	39–62	8–12	Enr. Parrotta *et al.* (1994)
id.	2 (M)	10000		94	9	Dif. Parrotta *et al.* (1994)
id.	2 (C)	5000		62	12	Dif. Parrotta *et al.* (1994)
			Myrica faya			
Hawaii				18		Inc. Vitousek and Walker (1989)

[a] Senegal M: Malika, site close to the sea; Senegal N: Notto, site distant from the sea.

[b] (M) monoculture of *C. equisetifolia*; (C) mixed stand of *C. equisetifolia* and *Eucalyptus robusta*.

[c] Methods of assessment: ARA, acetylene reducing activity; Dif., total N difference; Bal., balance studies; Enr., enrichment with ^{15}N labelled fertilizer (also called isotope dilution method); NA, ^{15}N natural abundance; Inc., increase of total N soil content. The results obtained through isotope methods either in Senegal or at Porto Rico are in close agreement with estimates made using the N difference method.

tion, diseases and enemies. Other factors can be involved such as age: N_2 fixation increases each year in young plantations, then, after 10–20 y, decreases with time for different reasons including the accumulation of available N in the soil.

TRANSFER OF FIXED N_2 TO THE SOIL AND COMPANION PLANTS

All cultivated soils are prone to losing nutrients, especially N, either by erosion, removal in crops, gaseous losses (denitrification and NH_3 volatilization), or leaching. In tropical soils N losses range from 20 to 40 kg ha^{-1} y^{-1} but they can be up to 70 kg ha^{-1} y^{-1}. The nutrient balance has to be restored by proper management practices (especially fertilization and recycling of agricultural wastes) and by exploiting the N_2 fixation process. Inputs from N_2 fixation are usually through introducing more annual or perennial legumes into farming systems. Actinorhizal plants are seldom used for this purpose in spite of the fact that their role in improving the soil fertility is clearly established in certain silvopastoral and agroforestry systems as shown by the three following examples.

Under a 2-year-old plantation (1200 trees ha^{-1}) of *Alnus acuminata* (syn. *A. jorullensis*) in the Colombian highlands the increase of soil N content has been estimated to be about 279 kg ha^{-1} (Carlson and Dawson, 1985). It is not yet known whether such an improvement of the soil N status results only from N_2 fixation or also from other processes, common to a number of trees, such as nutrient retrieval, reduction of losses from wind and water erosion. One undisputable fact is that, by introducing *A. acuminata* in cattle pastures, farmers in Costa Rica got a significant increase in the production of milk (Budowski, 1957, 1979).

Another well documented example of the ability of actinorhizal plants to improve soil is that of *Casuarina oligodon* in the highlands of Papua Guinea (Ataia, 1983; Thiagalingam, 1983; Bourke, 1985) and in Irian Jaya (Askin *et al.*, 1990). This species of *Casuarina* has been successfully introduced in agroforestry systems (annual and perennial food crop gardens) since 1960 and has expanded rapidly since about 1970.

Though carried out under a temperate climate (North America) the following experiment reported by Friedrich and Dawson (1984) is worth mentioning. Comparing soil N concentration in plots of a 14-year-old plantation of *Juglans nigra* mixed with different N_2-fixing species (*Alnus glutinosa*, *Elaeagnus umbellata*, *Robina pseudoacacia* and *Lespedeza striata*), the authors found that interplantings of *Juglans* with *Robinia* and *Elaeagnus* had the highest total N concentration in the top 30 cm soil, followed by *Alder*, *Lespedeza* and control plots: the overall mean N concentration in the horizon 0–30 cm (expressed in mg·N kg^{-1} soil, dry weight) was 1022 (j) for *Robinia*, 1006 (j) for *Elaeagnus*, 995 (jk) for *Lespedeza*, 936 (k) for *Alnus*, and 933 (k) for control plots (N concentrations followed by the same letter are not significantly different at $P = 0{\cdot}05$). *Juglans* size was greatest by far in *Elaeagnus* plots, where the actinorhizal plants not only improved the soil N status but also afforded shading and weed control. One complementary benefit following *Juglans–Elaeagnus* interplanting could be the reduction of the spread of spores of the foliar disease walnut anthracnose (Dawson, 1990). The benefits of interplanting valuable *Juglans nigra* with *Elaeagnus umbellata* are illustrated in Table 3.

Whereas it is fully acknowledged that *Alnus acuminata*, *Casuarina oligodon* and *Elaeagnus umbellata* significantly improve soil fertility and increase the productivity of associated plants, nobody has yet assessed the exact contribution of the N_2 fixation process alone. The reason is that assessing the amount of fixed N_2 transferred to soil and subsequently to non-N_2-fixing plants is difficult. However, this type of investigation has already been carried out successfully, using an isotope technique by Van Kessel *et al.* (1994) in the case of a perennial legume (*Leucaena leucocephala*). The major difficulty encountered results from the interference of two processes taking place in most tree ecosystems: redistribution of N in internal pools and recycling of fixed N_2. The first process is trivial in the case of young trees because of their relatively low biomass. As to the recycling of N, it can also be neglected but only when the decomposition rate of the litter is low.

Table 3. Average height (ht in m), stem diameter at breast height of 1·5 m (dbh in cm) and annual dbh growth rate for *Juglans nigra* interplanted with actinorhizal plants in Illinois[a] (Dawson, 1992)

Interplanted species					Average annual dbh growth rate		
	Age 14 y		Age 18y		Age (y)		
	ht (m)	dbh (cm)	ht (m)	dbh (cm)	0–14	14–18 cm y^{-1}	0–18
Elaeagnus umbellata	10·0	15	12·2	19	1·1	1·0	1·1
Alnus glutinosa	7·6	10	10·1	14	0·7	1·1	0·8
Control	3·4	4·9	4·9	8	0·4	0·6	0·4

[a] Twenty-four *J. nigra* spaced at 9·8 m × 3·7 m with three actinorhizal plants between, giving an overall spacing of 2·4 m × 3·7 m. Control plots without interplanting in a row.

Table 4. Propagation of actinorhizal plants by seeds (Seed), cuttings (Cut.), suckering (Suc.), air-layering (Air), stump sprouts (Spr,) and micropropagation (Mic.) (after MacDicken, 1994; Subba Rao and Rodríguez-Barrueco, 1995)

Species	Seed	Cut.	Suc.	Air	Spr.	Mic.
Alnus acuminata/jorullensis		●	●			
A. glutinosa	●			●	●	●
A. nepalensis	●					
Allocasuarina verticillata	●		●			●
Casuarina cristata	●		●			
C. cunninghamiana	●	●			●	
C. equisetifolia	●	●	◇	◇		●
C. glauca	●			●	●	●
C. junghuhniana	●	●	●			
Elaeagnus angustifolia	●	◇				●
Gymnostoma papuana	●	●				

● Generally successful.
◇ Infrequently successful.

Such an absence of recycling, which is characteristic of open ecosystems (Dommergues, 1995), was observed in *Casuarina equisetifolia* plantations established on the coastal sand dunes of Sénegal, whose soil is very poor in N (N < 0·01%) and where the decomposition of the litter is impeded by drought (mean annual rainfall is ca. 300 mm), the absence of an active soil microfauna, and nutrient deficiencies (especially P deficiency). In these plantations the accumulation rate of N in the soil and litter was estimated to be 23 kg ha^{-1} y^{-1} at one site by Dommergues (1963) and 75 kg ha^{-1} y^{-1} at other sites by Mailly and Margolis (1992). N balance studies confirmed that the observed accumulation of N resulted primarily from N_2 fixation.

More investigations are obviously required, especially in the tropics and subtropics, (i) to quantify the amount of fixed N_2 added to the soil N and N uptake by non-N_2-fixing companion plants and (ii) to evaluate the other benefits such as those resulting from the addition of organic matter, improvement of soil structure, reduction of erosion, shading, weed control on disease control.

SYSTEMS OF LAND USE AND MANAGEMENT

In addition to their ability of fix N_2, actinorhizal plants possess four essential traits which are less often found in legume trees:

(i) They are able to thrive in poor and wasted lands (which is not the case for a number of legume trees like *Leucaena* spp),

(ii) Actinorhizal plants are tolerant or semi-tolerant to a range of toxic pollutants. Thus *Alnus glutinosa* tolerates relatively high levels of boron, cadmium, lead and zinc (Wheeler and Miller, 1990). Like *Alnus glutinosa, Casuarina equisetifolia* forms good barriers for catching industrial dusts. Therefore actinorhizal plants would be prime candidates for achieving phytoremediation (Salt *et al.*, 1995) of polluted sites.

(iii) Some actinorhizal plants are adapted to environmental conditions that differ widely from those occurring in their native habitat. Thus *Casuarina glauca*, which is native to a narrow coastal belt of southeast Australia where annual rainfall averages 500 mm, thrives in Hawaii up to an altitude of 900 m and with annual rainfall as much as 4000 mm. The same species grows vigorously in Egypt with annual rainfall less than 50 mm, provided that it is correctly irrigated (El-Lakany, 1990, 1991). *Alnus glutinosa*, native to climates with severe cold, may perform well in tropical highlands where unseasonal cold can destroy other *Alnus* species (NRC, 1980). This wide adaptability is shared by other actinorhizal plants, especially *Casuarina cunninghamiana* and *C. junghuhniana*.

(iv) Actinorhizal plants are fairly resistant to pests and major diseases.

(v) In addition, actinorhizal plants are easily propagated by seed or through diverse methods of vegetative propagation including micropropagation (Table 4).

For all the reasons mentioned above actinorhizal plants can be successfully introduced in a number of systems of land use: production forestry (es-

Table 5. Management systems involving representative tropical, subtropical and mediterranean actinorhizal plants: production forestry (Prd.), agroforestry (Agr.), protective forestry (Prt.), reclamation forestry (Rcl.) and urban forestry (Urb.)

	Prd.	Agr.	Prot.	Rcl.	Urb.
Alnus acuminata	+	+	+	+	
A. nepalensis	+	+	+		
A. glutinosa	+[a]		+	+	
Allocasuarina verticillata	+				+
Casuarina cunninghamiana	+				+
C. equisetifolia	+[a]		+[a]	+	+
C. glauca	+	+	+[a]	+	+
C. junghuhniana	+	+	+	+	+
C. oligodon	+	+			
Elaeagnus angustifolia				+	+
E. umbellata	+[a]				
Myrica faya				+	
Hippophaë rhamnoides		+		+	

[a] Including mixed plantations with non-N_2-fixing trees.

pecially mixed-tree plantations), agroforestry (enriched fallows, alley cropping and intercropping), sylvopastoral systems, protective forestry (especially sand dune stabilization, windbreaks and control of water erosion), reclamation forestry (reclamation of eroded, salinized and wasted mine soils and phytoremediation), and urban forestry (amenity plantations in cities and recreational areas) (Table 5).

Examples of successes abound. Some have already been mentioned. The following should also be given:

—Increase of productivity of *Quercus robur* grown on lignite spoil banks at Santa Barbara (Italy) through its association with *Alnus cordata*, an actinorhizal plant which increases available N for associated timber trees both by its high capacity to fix N_2 (80% of plant N derived from N_2 fixation) and its low N uptake from soil (20% of plant N derived from soil) (Buresti *et al.*, 1991).

—Reduction of the volume of excess salinized drain water in the San Joachin Valley (California) by irrigating *Casuarina glauca* and *C. cunninghamiana* with this water (Merwin, 1990).

—Afforestation of clay and sand-filled reclaimed lands at Singapore with *Acacia auriculiformis*, *Paraserianthes falcataria* and *Casuarina equisetifolia* (Lee *et al.*, 1993).

—Rehabiliting quarry sites and limestone spoil from a cement factory near Mombasa, Kenya (Baobab Farm) by planting *Casuarina equisetifolia* (Baumer *et al.*, 1990).

—Protecting crops against wind by planting *Casuarina equisetifolia* windbreaks in China (Turnbull, 1983) or *Casuarina glauca* in Egypt (El-Lakany, 1983) and Tunisia.

—Stabilizing sand dunes in many countries such as China (Turnbull, 1983) or Senegal (Andéké-Lingui and Dommergues, 1983).

Many other success stories have been reported in the books and reviews of Midgley *et al.* (1983), NRC (1984), Dawson (1992), Pinyopusarerk and House (1993) and Subba Rao and Rodríguez-Barrueco (1995). Yet failures have been observed but infrequently reported. Some result from inherent characteristics of the actinorhizal plant to be planted, such as sensitivity of *Casuarina* to some pests (Hassan, 1990; Pinyopusarerk and House, 1993), sensitivity of *Hippophaë rhamnoides* to nematodes (F. Zoon, Ph.D. thesis University of Wageningen, 1995) or low salt tolerance of *Casuarina oligodon* (NRC, 1984). Other failures are the consequence of inappropriate management practices, a frequent situation when dealing with mixed plantations (Schlesinger and Williams, 1984). Finally many failures are caused by unexpected or disregarded soil constraints (especially nutrient deficiencies and drought) and the absence of compatible *Frankia* strains. These problems will be dealt with in the following section.

STRATEGIES FOR INCREASING N INPUTS FROM ACTINORHIZAL PLANTS

In actinorhizal plants the situation is similar to that encountered in legume trees: the amount of N_2 actually fixed is often lower than expected (values of the order of 10–20 kg N_2 fixed ha^{-1} y^{-1} are not infrequent), whereas losses from ecosystems are often much higher, as already stressed. Therefore it is mandatory to devise efficient strategies to increase the input of N, which involves not only the reduction of the effects of environmental constraints but also the establishment of a symbiosis with high symbiotic performance and a sufficient tolerance to the remaining environmental constraints, the main ones being: soil nutrient deficiencies and factors associated with soil acidity, salinity, excess of plant-available N in the soil, drought, enemies and diseases.

To attain this goal two strategies have to be adopted: the first one is to use proper management practices; the second one is to improve the performance of the N_2-fixing system.

Alleviating soil constraints through proper management practices

Soil nutrient deficiencies and acidity. Nutrient deficiencies are frequent when the plantations have been established on very poor soils, which is the case for a *Casuarina equisetifolia* plantation in Benin, West Africa (Zech and Kaupenjohann, 1990). Deficiencies appear quite often in soils whose nutrient reserves have been depleted by successive removal of forest products, including litter, often removed from *Casuarina* plantations in southern China (Diem and Dommergues, 1990). Replenishing soil reserves by proper addition of fertilizers, especially P, is an absolute requirement. Casuarinaceae potentially are well suited to utilize rock phosphates, since they require fairly large amounts of Ca and probably, like legumes (Giller and Cadisch, 1995), they could possibly acidify the soil.

Acidity is a major constraint to nodulation, because it affects the process of infection. Liming is often suggested to raise the soil pH, which has the advantage of supplying Ca and reducing Al toxicity. However, the cost of liming is often prohibitive and selection of acid tolerant host plants is preferable.

Drought. Water deficits affect symbiotic N_2 fixation through influences on host plant metabolism, nodulation and nodule function, as shown by various experiments with Casuarinaceae (Reddell, 1993). Since semi-arid and arid regions receive too little precipitation to ensure good plant growth and adequate N_2 fixation, irrigation is often required. A variety of irrigation systems have been developed, but most of them do not guarantee a sustained economic return. Therefore, low input practices are recommended, especially rainwater harvesting systems that have been successfully used to direct infrequent runoff into the rooting zone of trees or to assist groundwater recharge. Temporary watering may be necessary during the establishment phase of plantations to assist root systems in reaching permanently moist soil horizons. This practice is currently applied to ensure the success of *Casuarina equisetifolia* plantations on the Senegalese coast and *C. glauca* windbreaks in Egypt.

Soil pathogens. Among soil pathogens nematodes are probably the most dangerous, at least for some species of actinorhizal plants. Sterilization of nursery soils using simple methods such as solarization is therefore recommended; unfortunately such a measure is seldom applied.

Improving the performances of Frankia *and host plant*

The two main criteria for improvement are higher N_2 fixation (generally assessed in growth chamber or greenhouse) and, when environmental conditions cannot readily be altered, increased tolerance to environmental constraints. Examples illustrating these approaches are given below.

Development of higher N_2 fixation. It is now clear that the N_2-fixing potential depends on host plant genotype, symbiotic bacterial strain and their interactions. By selecting both partners of the symbiosis it is thus possible to increase the performances of N_2-fixing systems.

The usual screening procedures based on the exploitation of the variability of *Frankia* is currently used to improve the symbiotic performances (competitive ability and effectivity) of the actinomycete. Theoretically the techniques of molecular biology have great potential to achieve this goal. However, in spite of recent advances, practical results cannot be expected in the short term, because investigations on the transformation of *Frankia* still lag behind those concerning the rhizobial symbiosis and the streptomyces (Dawson, 1992; Benson and Silvester, 1993).

With the exception of some species like *Ceanothus* sp. (Nelson and Lopez, 1989), actinorhizal plants exhibit enormous variability, and exploitation of this is promising. Provenance selection should be performed as a first stage, followed by clonal selection. This procedure is facilitated by the fact that a number of actinorhizal plants are readily propagated vegetatively (Table 4), which allows for the development of micropropagation techniques (Duhoux *et al.*, 1993). Thus a highly effective N_2-fixing clone of *Casuarina equisetifolia* (clone β) obtained by screening a large number of seedlings according to their nodulation, was easily propagated by cuttings (Sougoufara *et al.*, 1987).

Whereas conventional plant breeding methods have been applied to improve growth of *Casuarina* at different sites (El-Lakany, 1983), improvement programs have not yet taken into account the N_2-fixing capability of the host (Diem and Dommergues, 1990).

Do host–strain interactions that may exist in legume N_2-fixing symbioses, also occur in actinorhizal symbioses? To elucidate this problem the following experiment was carried out. The objective was to compare the amount of N_2 fixed by nine combinations involving three clones of *Casuarina equisetifolia* and three strains of *Frankia.* Analysis of variance showed a very significant effect ($P < 0{\cdot}01$) of the actinorhizal clones and *Frankia* strains and a less significant effect ($P < 0{\cdot}05$) of the "*C. equisetifolia* clone × *Frankia* strain" interaction (Sougoufara *et al.*, 1992). Since the ranking of clones and strains was not affected by the "clone × strain" interaction in this experiment, the authors suggested that the identification of the best N_2-fixing combination "*C. equisetifolia* clone × *Frankia* strain" could be achieved through a simple procedure involving only two comparisons: comparison of the clones associated with one *Frankia* strain and comparison of the *Frankia* strains associated with one clone. Such a simplified procedure cannot be used when "actinorhizal plant genotype × *Frankia* strain" interactions are significant. This last situation probably exists, but has not yet been reported in the case of actinorhizal plants.

Development of insensivity to combined N (plant-available N). Field as well as most laboratory experiments indicate that nodulation and N_2 fixation are inhibited by combined N (that is the plant-available N in the soil) (Huss-Danell, 1990). However, a continuous supply of combined N in small doses, which were continuously increased to match the plant uptake, stimulated growth and N_2-fixation in *Alnus incana* seedlings (Ingestad, 1980). Field observations show that the nodule biomass is high in old *Alnus, Casuarina* and *Allocasuarina* plantations (several hundred kg ha^{-1}) in spite of the accumulation of plant-available N, whereas nodules tend to disappear under most ageing stands of legume trees. These observations would suggest that the actinorhizal plants mentioned above would be less sensitive to combined N than most legumes. However, this insensivity does not hold for all actinorhizal plants species; thus in *Hippophaë rhamnoides* vegetation the nodule numbers m^{-2} markedly decrease at higher ages of the plants (Stewart and Pearson, 1967: A.D.L. Akkermans, unpubl. Ph.D. thesis, University of Leiden 1971). In fact, recent investigations suggest that the reduction of the number of actinorhizal nodules in *H. rhamnoides* could result from the proliferation of plant parasitic nematodes following increased availability of N in the soil and increased food quality of plant cell contents and also from possible interactions between nematodes and root-rot fungi (Zoon, *loc.cit.*)

The development of actinorhizal genotypes tolerant of combined N is probably essential in some situations, especially in the presence of large amounts of combined N. Two approaches could be adopted to develop genotypes with this trait: screening genotypes for their ability to nodulate in the presence of combined N or for their ability to form aerial nodules, a possibility which has been already reported in *Casuarina cunninghamiana* and *C. glauca*; it has been postulated that aerial nodulation would make these host plants more independant of soil constraints and allow them to express their N_2-fixing potential even in soil with unfavorable characteristics, especially excess of combined N (Prin *et al.*, 1991).

Development of tolerance to acidity or alkalinity. Like a number of legumes, actinorhizal plants probably exhibit inter- and intraspecific variations in their adaptation to acidity or alkalinity. Actinorhizal plant selection in this direction would certainly be rewarding.

Development of tolerance to salinity. Casuarina glauca, and to a lesser degree *C. equisetifolia* have been used to reclaim salt-affected areas. Their tolerance can be enhanced by selection of the host (e.g. provenance screening); the role of associated *Frankia* appears to be negligible. *Frankia* strain Thr, poorly salt tolerant *in vitro*, appeared to improve N_2 fixation better than other strains (which were more salt tolerant *in vitro*) when associated with a provenance of *C. glauca* (E) known for its salt tolerance in the field (Girgis *et al.*, 1992).

Development of tolerance to drought. A number of actinorhizal plants are drought-resistant such as *Allocasuarina decaisneana, A. campestris, A. dielsiana, Casuarina obesa* and *C. cristata* ssp *pauper* (Reddell *et al.*, 1991), and South American Rhamnaceae. Some species, such as *Casuarina equisetifolia*, are able to obtain their moisture from foliar water absorption from dews or ocean sprays.

Usually *Alnus* spp have high water requirements but some, like *A. cordata*, are fairly drought resistant and others, like *A. acuminata*, are able to meet their moisture requirements from mists and clouds through the dry season (Russo, 1994). Breeding techniques have been successfully used to improve drought tolerance of *Casuarina* (El-Lakany, 1983).

Development of resistance to diseases and pests. Though actinorhizal plants are reputed to be rather resistant to pathogenic fungi, bacteria, viruses, insects and nematodes, one cannot exclude possible damage by these agents (Hassan, 1990; Pinyopusarerk and House, 1993). One of the most elegant approaches to this problem is to introduce resistance genes into the host plants. This is no longer a remote possibility since gene transfer systems for Casuarinaceae (Franche *et al.*, 1994) and *Alnus glutinosa* (Mackay *et al.*, 1988) have already been developed (whereas such systems are not yet available in *Frankia*). One of the first targets will probably be the introduction of insect resistance genes into species of *Casuarina* (Franche *et al.*, 1994; Diouf *et al.*, 1995).

INOCULATION WITH SELECTED STRAINS OF *FRANKIA* AND MYCORRHIZAL FUNGI

As in the case of legumes, the need for inoculation depends mainly on the specificity of the host plant and on the size of the resident population of the symbiotic compatible bacteria. The distinction between promiscuous (also called non-specific) and non-promiscuous (also called specific) species is well known for legumes and also holds for actinorhizal trees. Promiscuous actinorhizal genera, i.e. plants which enter into symbiosis with a broad range of *Frankia*, are *Myrica* (Myricaceae) and to a lesser extent *Alnus* (Betulaceae) and *Gymnostoma* (Casuarinaceae). Specific actinorhizal genera are *Allocasuarina* and *Casuarina* (Maggia and Bousquet, 1994). Response to inoculation is to be expected more frequently in specific actinorhizal plants than in non-specific ones.

The size of the resident soil-borne compatible *Frankia* population is highly variable. There is no general rule to predict it and therefore it is necessary to evaluate the number of infective units of *Frankia* using methods such as those proposed by Arveby and Huss-Danell (1988) or Dawson *et al.* (1989). When *Frankia* infective units are few or absent the response to inoculation is spectacular provided there is no major limiting factor. A clear positive response to inoculation was recorded in the semi-arid and arid soils of Senegal, Egypt and Zimbabwe, which are devoid of *Casuarina*-compatible *Frankia*. By contrast, inoculating *Alnus glutinosa* planted in soils already harboring *Alnus*-compatible *Frankia* did not significantly affect host growth (Table 6).

The development of *Frankia* inoculants has been delayed for a number of years because isolating *Frankia* is sometimes very difficult and the culture of this microorganism is not easy because *Frankia* grows slowly with doubling times of 15 h (Schwencke, 1991) and low increase of biomass with respect to the amount of inoculum. The pattern of growth varies with the inoculum density (Frioni *et al.*, 1994), medium composition, and degree of agitation (Benson and Silvester, 1993). Advances have been made recently in the mass culture of *Frankia* (Diem and Dommergues, 1990) and the use of polymeric carriers (Diem *et al.*, 1988) which allows the production of *Frankia* inoculants of high quality. The most convenient formulation of *Frankia* inoculum is obtained by entrapping a *Frankia* culture containing a large number of spor-

Table 6. Effect of inoculation with pure *Frankia* cultures on field-grown *Casurina cunninghamiana* in Zimbabwe (Reddell *et al.*, 1988), *Casuarina equisetifolia* in Senegal (Sougoufara *et al.*, 1989) and *Alnus glutinosa* in France (Prat, 1992)

Species (provenance or clone)	Treatment	Age	Height (m)	Weight (g tree^{-1})	Volume^a (m^3 ha^{-1})
Casuarina cunninghamiana (Zimbabwe)					
Gympie	Inoc.	41 months			111
id.	Uninoc. + N	id.			54
Mareeba	Inoc.	id.			69
id.	Uninoc. + N	id.			41
Mt Morgan	Inoc.	id.			84
id.	Uninoc. + N	id.			59
Casuarina equisetifolia (Senegal)					
Senegal	Inoc.^{b}	2 y	3.1	2846	
id.	Uninoc.	2 y	2·9	2025	
id.	Inoc.^{b}	3 y	5·7	4607	
id.	Uninoc.	3 y	5·0	3291	
Alnus glutinosa (France)					
Najybajom	Inoc.	4 y	2·4		
id.	Uninoc.	id.	1·8		
clone 11	Inoc.	id.	2·0		
id.	Uninoc.	id.	1·3		
clone 142-2	Inoc.	id.	2·1		
id.	Uninoc.	id.	2·0		

[a] Wood volume expressed as m^3 ha^{-1} was estimated assuming $V = 1/3\ d^2h$ where d = stem diameter at ground level and h = tree height. For example the mean diameter of inoculated Gympie *Casuarina cunninghamiana* was 0·225 m and their height was 8·2 m with a stocking rate of 800 trees ha^{-1} So $V = 1/3\ (0{\cdot}225)^2 \times 8{\cdot}2 \times 800 = 111$ m^3 ha^{-1}.

[b] Inoculation with *Frankia* entrapped in alginate beads (2-year storage).

The effect of inoculation was significant for *C. cunninghamiana* (tree volume), *C. equisetifolia* (weight but not height) and not significant for *A. glutinosa*.

angia in alginate beads, with kaolinite added to the gel. This type of inoculant is not only easy to transport, it also has a remarkably long shelf life (Diem and Dommergues, 1990). An example of field inoculation with *Frankia* entrapped in alginate beads is given in Table 6.

In P-deficient soils, dual inoculation with *Frankia* and VA endomycorrhizal fungi can improve P uptake by increasing the volume of soil explored and subsequently can enhance N_2 fixation and growth of actinorhizal plants (Diem and Gauthier, 1982; Gardner *et al.*, 1984). Since mycorrhizae are also assumed to improve drought resistance of host plants by increasing water supply and water use efficiency, inoculating actinorhizal plants with selected mycorrhizal strains can also be beneficial under arid and semi-arid conditions. Inoculants obtained by entrapping chopped roots of VA mycorrhizal plants with their spores in alginate beads are as efficacious as the *Frankia* inoculants prepared according to the same procedure (Ganry *et al.*, 1985). It must be noted that a positive response to inoculation can be expected only in soils with very low populations of VA endomycorrhizal fungi, a situation which is found in partially sterilized nursery soils.

Records of ectotrophic mycorrhizal associations with tropical actinorhizal plants are still few (an example is that of *Pisolithus* associated with *Allocasuarina*) and further fundamental investigations are obviously required before developing inoculants carrying ectomycorrhizal fungi adapted to specific actinorhizal plants grown in certain ecological conditions.

CONCLUSION

In spite of their remarkable adaptability and their oustanding performance in harsh sites, actinorhizal plants have not yet been exploited sufficiently. The benefits that they can provide can be dramatically increased in the near future provided that the following strategies are adopted:

(i) Optimizing actinorhizal N_2 fixation in the field using the approaches described in detail above.

(ii) Introducing actinorhizal plants already known for their performance into countries and ecosystems where they are now absent. Thus tropical *Alnus* could be planted in mixed plantations and in pastures in African and Madagascan highlands. *Casuarina oligodon*, which is used as a soil improver in Papua New Guinea and has been successfully introduced in Uganda (Peden *et al.*, 1993) could be expanded to other African countries and probably to some parts of South America. *Casuarina equisetifolia* and *C. glauca* plantations could be enlarged along most African coasts, providing much needed fuel to the inhabitants and thus limiting indirectly the process of desertification following the destruction of the last woodlands.

(iii) Domesticating a number of species that have been neglected or overlooked in most countries, such as *Coriaria sinica*, a deciduous bush grown as a source of green manure in the Hunan province (Dommergues, 1987); *Coriaria nepalensis*, a potential candidate for revegetating and controlling erosion in areas overcrowded by cattle (Akkermans *et al.*, 1985); *Myrica esculenta*, a tree which grows in tropical and subtropical climates of SE Asia and which is associated with pines and oaks in the forests of Himalaya (G. Lim, pers. commun.) *Myrica faya* used as understory in pine plantations in Portugal (Bermúdez de Castro, 1977), and many other tropical *Myrica* species (Mercado, 1978).

(iv) Exploiting the exceptional ability of most actinorhizal plants to contribute to the rehabilitation of wasted lands and possibly to the phytoremediation of polluted sites.

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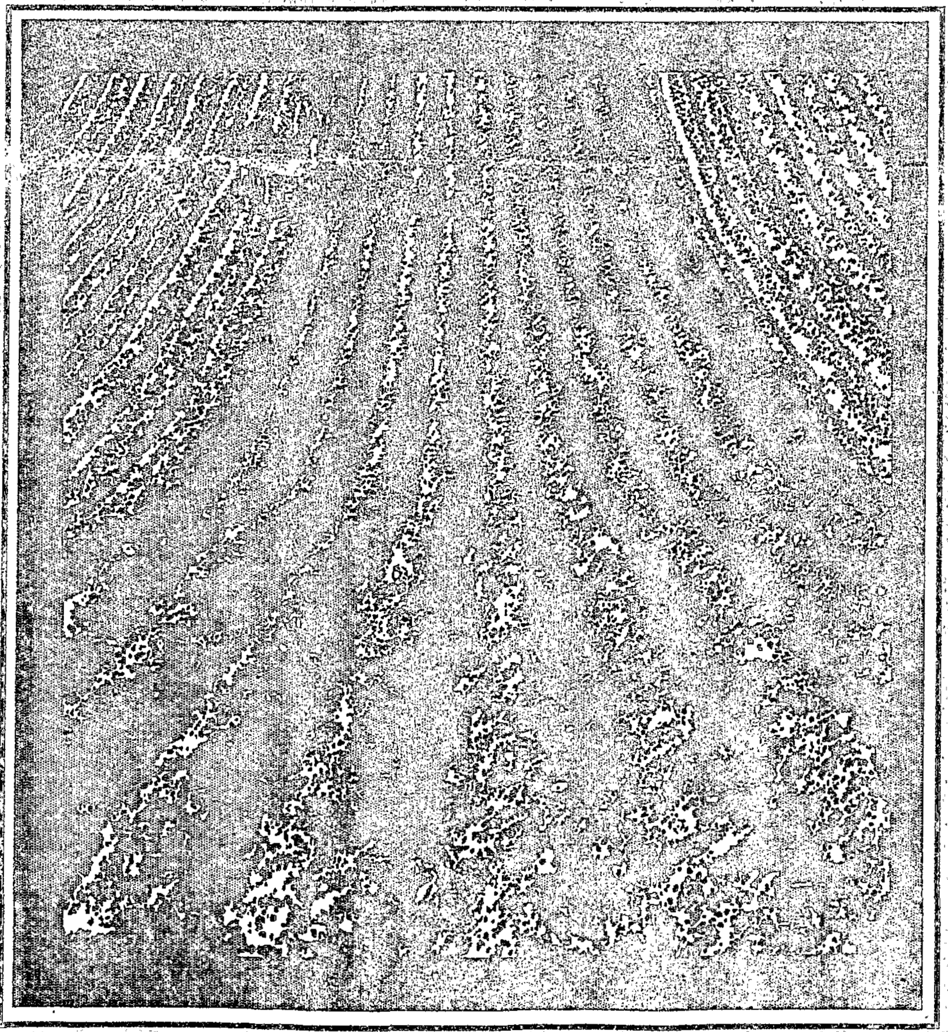

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