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IMPORTANCE AND DIVERSITY OF *FRANKIA-CASUARINACEAE SYMBIOSIS* IN NEW CALEDONIA.

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SUMMARY.

New Caledonia has for its small area (19.000 km^2) a considerable concentration of endemic Casuarinaceae. There are recorded 8 species of *Gymnostoma* (more than 40% of the world total) and 1 species of *Casuarina*. All these species appear as nodulated and perfectly adapted, being undemanding for major elements and insensitive to soil toxicities, to the poor and unbalanced soils on which they grow. The Casuarinaceae often dominate the pioneer or forest-margin formations in which they occur.

Their diversity and their ecological specificities thus confer on the Casuarinaceae endemic in New Caledonia a real interest for use in rehabilitation of degraded soils and mined areas.

KEYWORDS : Casuarinacae, *Gymnostoma*, endemic, ultramafic rocks, New Caledonia.

RESUME.

Compte tenu de sa faible superficie (19000 km^2) la Nouvelle-Calédonie possède une forte concentration en Casuarinaceae endémiques. On dénombre 8 espèces de *Gymnostoma* (plus de 40 % des espèces mondiales) et 1 espèce de *Casuarina*. Toutes ces espèces se sont révélées être nodulées et parfaitement adaptées aux sols pauvres et déséquilibrés sur lesquels elles poussent car peu exigentes en éléments minéraux majeurs et peu sensibles à la toxicité du sol. Les Casuarinaceae présentent un caractère dominant dans les formations pionnières ou de lisière où elles se développent.

Les Casuarinceae endémiques à la Nouvelle-Calédonie présentent donc, du fait de leur diversité et de leurs particularités écologiques, un intérêt indéniable en ce qui concerne leur utilisation pour la réhabilitation des sols dégradés et des déblais miniers.

1 - INTRODUCTION.

The Casuarinaceae can thanks to their nitrogen-fixing symbiosis with *Frankia* grow on soils of low fertility. Their species present in tropical areas have an important potential for firewood production, agroforestry and the rehabilitation of degraded soils (Midgley et al., 1983).

The Casuarinaceae are represented (Johnson 1980, 1982) in New Caledonia by 8 endemic species of *Gymnostoma* and 2 species of *Casuarina* : *C. collina*, endemic, and *C. equisetifolia*, native but widespread in seashore formations elsewhere.

New Caledonia, considering its small area (19000 km^2) appears to have the greatest concentration of Casuarinaceae in the world, particularly for *Gymnostoma* (8 of the 18 known species).

The genus *Gymnostoma* is widespread with 18 species in Australia, Malaysia and Melanesia (Dilcher et al., 1990). It has however been little studied, the only serious work being by Racette and Torrey (1989) on the symbiosis between *Gymnostoma papuanum* and *Frankia*.

The present study aims to cover the different species of Casuarinaceae endemic in New Caledonia and to describe their ecology.

2 - MATERIAL AND METHODS.

The species studied are *Casuarina collina* Poisson, *Gymnostoma chamaecyparis* (Poisson) L. Johnson, *G. deplancheanum* (Miquel) L. Johnson, *G. glaucescens* (Schlechter) L. Johnson, *G. intermedium* (Poisson) L. Johnson, *G. leucodon* (Poisson) L. Johnson, *G. nodiflorum* (Thunberg) L. Johnson, *G. poissonianum* (Schlechter) L. Johnson and *G. webbianum* (Miquel) L. Johnson.

Populations of each of these species have been located, the importance of symbiotic actinomycete root nodules being estimated and the environmental conditions analysed.

For each species 6 nodulated plants 1-2 m high were taken in a representative population. The different organs of each plant (green parts, stem + branches, roots, root nodules) were separated and weighed after drying to constant weight at 60°. The mineral composition of each sample reduced to powder, and that of the soil around the root systems, were determined by the laboratoire d'analyse du Centre ORSTOM de Nouméa using the methods described by Pétard (1991).

For comparison, samples of the ubiquitous pioneer species *Alphitonia neo-caledonica* (Schlechter) Guillaumin, a non-nodulated Rhamnaceae, taken whenever possible in each station, were treated and analysed as for the species of Casuarinaceae.

3 - R E S U L T S.

3.1. Distribution and ecology.

The various species are heliophilic and gregarious. *Gymnostoma chamaecyparis*, *G. deplancheanum*, *G. leucodon* and *G. poissonianum* are limited to the massifs of ultramafic rocks ("terrains miniers") and *G. intermedium* has been found once only on another substrate, at an altitude of 950 m on the summit of the Roche Ouaième. *Casuarina collina*, *Gymnostoma webbianum* and *G. nodiflorum* occur on varied geological substrates, the last mainly away from ultramafic rocks.

Gymnostoma chamaecyparis and *G. deplancheanum* belong to typical maquis and to maquis passing into forest on ultramafic rocks. The former is associated with hypermagnesian soils usually below 600 m altitude. The second is found in the Great Southern Massif on gravelly or concretionary desaturated ferralitic ferritic soils at altitudes between 200 and 1000 m.

Casuarina collina, *Gymnostoma leucodon*, *G. webbianum* and *G. nodiflorum* find their ecological optima in riverside formations. *G. leucodon* is strictly localized in the Great Southern Massif from which *G. nodiflorum* is absent.

Finally, *G. glaucescens*, *G. intermedium* and *G. poissonianum* behave more than the others as forest species. They form on varied ferralitic ferritic soils the upper layer of dense rainforest whose ecological significance is not as yet fully understood but which may represent secondary formations evolving very slowly. *G. intermedium*, often found above 700 m, is rather definitely a mountain species.

3.2. Nodulation.

The aptitude for nodulation of the different species of Casuarinaceae has been studied in their natural ecological conditions. A study of 727 trees, of an average height of 1-2 m, shows that all the species are nodulated. Nodulation percentages (Table 1) range from 28% for *Gymnostoma nodiflorum* to 77% for *Casuarina collina*.

Nodules form 1.3 % of the total weight of the plant for *Casuarina collina* and from 0.3 % to 1.6 % for the species of *Gymnostoma*.

3.3. Plant-soil relationships.

3.3.1. Mineral composition of soils at the different stations.

The mineral composition of soils in different stations where Casuarinaceae were sampled is shown in Table 2.

All the soils are poor in phosphorus, potassium and sodium. The deficiency in these elements is more marked in the soils derived from ultramafic rocks than in that on sedimentary rocks (station of *G. nodiflorum*). Magnesium is the most abundant element among the exchangeable bases. The Ca/Mg ratio, which determines (Jaffré, 1976) the uptake of calcium in slightly desaturated soils derived from ultramafic rocks is thus highly unfavorable in the soil of the *G. chamaecyparis* station, and moderately unfavorable in those of the stations of *G. glaucescens, G. leucodon, G. poissonianum* and *G. webbianum*.

Nitrogen contents of the soils are very variable. They are unfavorable in the stations of *C. collina, G. deplancheanum, G. leucodon* and *G. poissonianum*, and fairly high in the others. The highest value (2.53 °/oo) was found in the *G. chamaecyparis* station. Organic matter, the source of nitrogen, tends when not carried away by water action to form a poorly decomposed layer of litter below the Casuarinaceae. C/N ratios above 15 for the various stations studied indicate that organic decomposition is slow and nitrogen poorly available in these types of soil.

Nickel contents, relatively high in all the soils derived from ultramafic rocks, range from 0.2 % in the *G. deplanchenum* station to 0.87 % in that of *G. poissonianum*. Finally, manganese contents are higher than those usually met with in these soils. The highest values occur in the soils of the station of *G. chamaecyparis* and that of *G. intermedium*. Manganese, because of differences in pH, is less available in the *G. chamaecyparis* station (pH = 6.7) ;than in that of *G. intermedium* (pH = 5.13).

3.3.2. Mineral composition of green parts.

The contents of mineral elements in the green parts of the different species have been compared with the averages for a large number of species associated to various conditions of soil and vegetation on ultramafic rocks (Jaffré, 1980). The results are shown in Tables 3, 4 and 5.

3.3.2.1. Casuarinaceae in maquis on ultramafic substrates.

The green parts of *G. deplancheanum* and *G. chamaecyparis* (Table 3) have, except for calcium in the former and sodium in both, lower contents of major elements than the average for shrubby dicotyledons growing in the same soils.

Manganese and nickel contents for these 2 *Gymnostoma* species are lower than those of the average for shrubby dicotyledons growing in the same edaphic conditions.

3.3.2.2. Casuarinaceae in forest or tall maquis.

The contents of major mineral elements of the green parts of forest species (*G. glaucescens, G. intermedium* and *G. poissonianum*) are shown in Table 4. These contents, except for calcium in *G. glaucescens* and sodium in all three species, are lower than the average for shrubby dicotyledons in tall maquis on colluvial ferralitic ferritic soils, and to that for forest dicotyledons on ultramafic rocks.

Nickel contents are relatively low for the three *Gymnostoma* species ; those of manganese are low for *G. poissonianum,* medium for *G. glaucescens* and relatively high for *G. intermedium.*

3.3.2.3. Streamside Casuarinaceae.

The mineral composition of the green parts of Casuarinaceae associated mainly with water-courses (*C. collina, G. leucodon, G. nodiflorum* and *G. webbianum*), compared with that of forest dicotyledons on ultramafic rocks, is shown in Table 5. Calcium, potassium and magnesium contents of the four Casuarinaceae are relatively low and below those of forest dicotyledons on ultramafic rocks. The position is reversed for nitrogen and phosphorus contents of *C. collina* and *G. nodiflorum* as also for nitrogen in *G. leucodon* and sodium in *G. nodiflorum.*

3.3.3. Mineral composition of whole plants.

The mineral composition of whole plants of each species of Casuarinaceae and that of a reference species (*Alphitonia neo-caledonica*) when present in the same station have been calculated from the composition and the determined weights of the different parts. The results are shown in Table 6.

Contents of potassium and phosphorus are low in all cases, and for a given station lower with the Casuarinaceae than with *Alphitonia neo-caledonica*. The highest concentrations of these elements are found with *C. collina* (240 ppm of P. and 0.38 % of K) and with *G. nodiflorum* (360 ppm of P. and 0.29 % of K).

Concentrations of calcium are relatively low but generally higher for a given station with the Casuarinaceae than with *Alphitonia*. The highest concentrations were recorded with *G. glaucescens* (1.28 %) and *G. deplancheanum* (1.12 %), all other species having calcium contents below 1 %.

Concentrations of magnesium are generally, for a given station, of the same order of magnitude with the Casuarinaceae as with *Alphitonia*. The highest level is found with *G. chamaecyparis* (0.22 %) which occures on the soil richest in magnesium.

The Ca/mg ratio is above 3 in all the Casuarinaceae in spite of an unbalance between these two elements in certain soils. This shows that these species reconstitute a normal Ca/Mg ratio in their tissues.

Sodium contents of Casuarinaceae are in general relatively high and in all cases above those of *Alphitonia neo-caledonica*.

Nitrogen contents of Casuarinaceae are above those of the reference plant for *C. collina* and *G. leucodon*, essentially the same for *G. webbianum*, *G. chamaecyparis* and *G. intermedium*, and lower for *G. deplancheanum*. The highest values occur with *C. collina* (0.91 %) and *G. nodiflorum* (0.86 %), the lowest with *G. intermedium* (0.41 %).

4 - DISCUSSION AND CONCLUSION.

Study of the distribution and the ecology of the different species of Casuarinaceae endemic to New Caledonia shows them to be particularly associated with outcrops of ultramafic rocks, on which *G. chamaecyparis, G. deplancheanum, G. glaucescens* and *G. leucodon* occur exclusively and *G. webbianum* and *C. collina* are well represented. Only *G. nodiflorum* is found mainly outside ultramafic areas.

It is probable that the heliophilic and pionnering nature of the Casuarinaceae implies their preference for open (normal maquis or tall maquis) or marginal (streamside or replacement growth in disturbed areas) plant communities.

The minera composition of green parts of the different species shows no sharp difference between the Casuarinaceae and other species of ultramafic areas. Their contents of P, K and Ca are low, as is that of nickel in relation to its level in the soil.

Manganese contents, though fairly high in *G. poissonianum*, are not at all exceptional for plants growing on desaturated ferralitic ferritic soils derived from ultramafic rocks. Finally, the relatively high sodium content of most casuarinaceae seems the only unusual feature compared with other species of ultramafic areas.

As far as nitrogen is concerned, nodulation of the *Gymnostoma* species scarcely involves any increase in their contents of this element.

Thus the Casuarinaceae in maquis and in forest away from water-courses show no distinction in nitrogen content from other species occurring in the same plant associations. An increase in nitrogen content above the average value for other dicotyledons appears only in the streamside species of Casuarinaceae and particularly in *C. collina* which in spite of very low soil levels of nitrogen shows the highest tissue contents.

The Casuarinaceae studies seem on the whole perfectly adapted, through their modest requirements for major elements and low sensitivity to soil toxicity, to the poor and unbalanced soils on which they grow. It remains however possible that unfavorable edaphic conditions may have a negative effect on nodulation efficiency.

The characteristic dominance, both in size and in biomass per individual plant, of the Casuarinaceae in the pioneer or marginal formations where they grow, should be emphasized. Their special nutrition, and particularly nitrogen fixation, affects the growth rate rather than the concentration of mineral elements in the plant, except for *Casuarina collina* which combines rapid growth with a high nitrogen content. This is well illustrated by *G. chamaecyparis* and *G. deplancheanum*, both with tissues relatively poor in mineral elements, which always overtop in the secondary formations where they grow most other species of the same age.

The endemic Casuarinaceae of New Caledonia thus show by their diversity and their special ecological characteristics, a real potential for use in the rehabilitation of degraded soils and of mined areas. The endemic species of *Gymnostoma*, some limited to ultramafic rocks, might offer a source of highly original strains of *Frankia*.

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Table 1 : Field nodulation of Casuarinaceae species in New Caledonia

Species	% of nodulation	% of plant dry weight
Casuarina		
C.collina	77 (82) (1)	1.3 ± 0.5 (2)
Gymnostoma		
G.deplancheanum	29 (215)	1.3 ± 0.5
G.poissonianum	47 (72)	0.8 ± 0.4
G.chamaecyparis	38 (87)	1.6 ± 1.1
G.intermedium	45 (49)	0.8 ± 0.3
G.nodiflorum	28 (50)	1.5 ± 0.5
G.glaucescens	39 (59)	0.6 ± 0.3
G.webbianum	59 (75)	0.3 ± 0.1
G.leucodon	47 (38)	0.9 ± 0.6

(1) Number of plants tested
(2) Mean of 6 trees

Table 2 : Chemical soil composition at different sampling stations for Casuarinaceae

Species	Total element (1)								Echangeable base (2)			
	pH	N mg/g	P ppm	K %	Ca %	Mg %	Ni %	Mn %	K	Ca	Mg	Na
Casuarina :												
C.collina	6.6 ± 0.3	0.58 ± 0.35	68 ± 12	0.036 ± 0.019	0.18 ± 0.16	2.86 ± 0.52	0.60 ± 0.19	0.38 ± 0.07	0.09	0.61	3.87	0.08
Gymnostoma :												
G.chamaecyparis	6.7 ± 0.3	2.53 ± 0.6	52 ± 13	0.032 ± 0.009	0.08 ± 0.06	3.98 ± 1.24	0.42 ± 0.07	0.56 ± 0.06	0.19	1.59	57.47	0.37
G.deplancheanum	4.7 ± 0.2	0.99 ± 0.5	143 ± 28	0.010 ± 0.004	<0.01	1.11 ± 0.04	0.20 ± 0.03	0.20 ± 0.05	0.06	0.67	0.42	0.12
G.glaucescens	5.3 ± 0.8	2.28 ± 0.60	113 ± 17	0.012 ± 0.009	<0.01	1.89 ± 0.56	0.69 ± 0.11	0.57 ± 0.20	0.19	0.60	2.25	0.20
G.intermedium	5.1 ± 0.5	1.69 ± 0.33	93 ± 11	-	<0.01	1.81 ± 0.47	0.71 ± 0.08	0.54 ± 0.23	0.20	0.80	1.12	0.22
G.leucodon	6.4 ± 0.2	0.73 ± 0.25	64 ± 5	0.017 ± 0.005	0.06 ± 0.05	2.97 ± 0.05	0.30 ± 0.07	0.26 ± 0.04	0.06	0.20	3.20	0.08
G.poissonianum	6.9 ± 0.2	0.55 ± 0.14	62 ± 19	0.017 ± 0.005	0.25 ± 0.09	8.52 ± 2.19	0.87 ± 0.12	0.48 ± 0.10	0.08	1.36	6.40	0.11
G.webbianum	5.8 ± 0.5	1.68 ± 0.82	171 ± 38	0.014 ± 0.006	<0.01	3.63 ± 1.01	0.52 ± 0.15	0.43 ± 0.15	0.16	1.19	5.00	0.15
G.nodiflorum	5.6 ± 0.3	1.44 ± 0.2	350 ± 60	0.031 ± 0.005	2.05 ± 0.06	1.82 ± 0.05	0.016 ± 0.002	0.06 ± 0.01	0.18	5.69	3.86	0.17

(1) Mean of 6 values ; (2) Mean of 2 values (me/100g)

Table 3 : Chemical composition of green tissues of Gymnostoma species in maquis on ultramafic substrates

Species	Green tissues							
	N %	P ppm	K %	Ca %	Mg %	Na %	Mn ppm	Ni ppm
On hypermagnesian soil								
G.chamaecyparis	0.81 ± 0.06	150 ± 20	0.29 ± 0.07	0.62 ± 0.14	0.37 ± 0.07	0.23 ± 0.03	70 ± 29	57 ± 23
Mean of 100 dicotyledons	1.03	340	0.81	1.04	0.51	0.16	270	110
On desaturated ferralitic ferritic soil								
G.deplancheanum	0.81 ± 0.03	160 ± 10	0.52 ± 0.11	1.17 ± 0.08	0.21 ± 0.04	0.48 ± 0.5	535 ± 427	15 ± 5
Mean of 100 dicotyledons	0.91	320	0.59	1.10	0.24	0.21	950	28

Table 4 : Chemical composition of green tissues of Gymnostoma species in forest or tall maquis

Species	Green tissues							
	N %	P ppm	K %	Ca %	Mg %	Na %	Mn ppm	Ni ppm
G. glaucescens	0.96 ± 0.07	130 ± 10	0.70 ± 0.06	1.12 ± 0.19	0.19 ± 0.03	0.62 ± 0.10	539 ± 293	19 ± 10
G.intermedium	0.81 ± 0.07	140 ± 10	0.42 ± 0.07	0.92 ± 0.16	0.18 ± 0.05	0.36 ± 0.05	2913 ± 1181	14 ± 3
G.poissonianum	0.91 ± 0.06	190 ± 30	0.50 ± 0.15	0.82 ± 0.13	0.28 ± 0.04	0.27 ± 0.04	67 ± 23	15 ± 4
Mean of 118 dicotyledons of forest on ultramafic soil	1.34	440	0.86	1.55	0.49	0.25	250	110
Mean of 72 dicotyledons of tall maquis	1.02	310	0.73	1.04	0.33	0.24	600	90

Table 5 : Chemical composition of green tissues of streamside Casuarinaceae

Species	Green tissues							
	N %	P ppm	K %	Ca %	Mg %	Na %	Mn ppm	Ni ppm
C.collina	1.60 ± 0.19	470 ± 110	0.53 ± 0.08	0.93 ± 0.13	0.28 ± 0.04	0.21 ± 0.06	341 ± 94	52 ± 14
G.leucodon	1.38 ± 0.07	160 ± 10	0.42 ± 0.04	0.95 ± 0.10	0.16 ± 0.02	0.26 ± 0.09	177 ± 48	47 ± 14
G.nodiflorum	1.57 ± 0.06	640 ± 80	0.56 ± 0.06	0.65 ± 0.07	0.19 ± 0.01	0.56 ± 0.05	183 ± 26	9 ± 2
G.webbianum	1.14 ± 0.11	240 ± 20	0.60 ± 0.07	0.73 ± 0.14	0.20 ± 0.04	0.23 ± 0.05	458 ± 235	20 ± 5
Mean of 118 dicotyledons of forest on ultramafic soil	1.34	440	0.86	1.55	0.49	0.25	250	110

Table 6 : Nitrogen and mineral content of nodulated Casuarinaceae and Alphitonia neocaledonica (Rhamnaceae) in different localities. (mean of 6 plants)

Localities and species	Nitrogen and mineral content in plant					
	N %	P ppm	K %	Ca %	Mg %	Na %
Riviere des Pirogues						
Alphitonia	0.45 ± 0.10	130 ± 40	0.42 ± 0.11	0.48 ± 0.14	0.13 ± 0.01	0.04 ± 0.02
G.leucodon	0.68 ± 0.07	100	0.22 ± 0.02	0.78 ± 0.13	0.07 ± 0.01	0.11 ± 0.02
C.collina	0.91 ± 0.12	240 ± 70	0.38 ± 0.06	0.79 ± 0.10	0.17 ± 0.04	0.11 ± 0.03
Plaines des Lacs						
Alphitonia	0.72 ± 0.08	140 ± 10	0.38 ± 0.06	0.99 ± 0.29	0.08 ± 0.02	0.06 ± 0.01
G.deplancheanum	0.55 ± 0.04	100 ± 20	0.25 ± 0.04	1.12 ± 0.4	0.12 ± 0.02	0.27 ± 0.03
Riviere Bleue						
Alphitonia	0.41 ± 0.05	100	0.28 ± 0.04	0.41 ± 0.08	0.10 ± 0.03	0.03 ± 0.01
G.webbianum	0.43 ± 0.06	70 ± 20	0.23 ± 0.06	0.72 ± 0.07	0.11 ± 0.05	0.08 ± 0.01
Tontouta						
Alphitonia	0.44 ± 0.04	120 ± 100	0.26 ± 0.05	0.59 ± 0.13	0.21 ± 0.03	0.01
G.chamaecyparis	0.49 ± 0.07	90 ± 20	0.17 ± 0.05	0.66 ± 0.14	0.22 ± 0.03	0.12 ± 0.02
Dzumac 1						
Alphitonia	0.38 ± 0.04	110 ± 20	0.30 ± 0.03	1.28 ± 0.14	0.09 ± 0.02	0.02 ± 0.01
G.intermedium	0.41 ± 0.03	80 ± 10	0.18 ± 0.03	0.86 ± 0.08	0.08 ± 0.01	0.13 ± 0.02
Dzumac 2						
G.poissonianum	0.47 ± 0.05	90 ± 10	0.25 ± 0.08	0.61 ± 0.07	0.13 ± 0.02	0.12 ± 0.02
Etoile Filante						
G.glaucescens	0.44 ± 0.05	< 50	0.27 ± 0.06	1.28 ± 0.11	0.08 ± 0.11	0.22 ± 0.07
Ciu						
G.nodiflorum	0.86 ± 0.08	360 ± 110	0.29 ± 0.02	0.52 ± 0.03	0.12 ± 0.03	0.23 ± 0.02