Cluster root formation by *Gymnostoma papuanum* (Casuarinaceae) in relation to aeration and mineral nutrient availability in water culture

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The term cluster root is used to refer to a dense cluster of determinate lateral roots (rootlets), in preference to the terms proteoid root and proteoid-like root used by other authors. Cluster roots are often formed by the actinorhizal plant *Gymnostoma papuanum*. In water culture, cluster root formation by *G. papuanum* was influenced by aeration, phosphorus level, and nitrogen source. Aeration was a critical factor, with nonaerated rooted cuttings having far fewer cluster roots than aerated ones. Phosphorus deficiency was the single nutrient deficiency that led to increased cluster root formation. Seedlings, grown under conditions of either low (0.8 mg L^{-1}) or no phosphorus, responded by devoting a greater portion of root growth to the production of cluster roots, with no overall reduction in root growth for 6 weeks. The response to varying phosphorus level was modified by providing nitrogen in different forms. Supplying nitrogen as ammonium resulted in low levels of cluster root formation. Supplying nitrate to nodulated seedlings led to an increase in cluster root formation in comparison with plants that depended solely upon dinitrogen fixation by *Frankia*. Greatest cluster root formation occurred on plants grown in aerated water cultures supplied with nitrate and with little or no phosphorus.

Key words: *Gymnostoma papuanum*, cluster roots, proteoid roots, phosphorus deficiency.

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Les auteurs utilisent le terme racines groupées (« cluster root ») préférentiellement au terme racines protéoïdes ou de forme protéoïdes, utilisés par d'autres auteurs pour désigner des amas denses de racines latérales déterminées (radicelles). Les racines groupées sont fréquentes chez la plante actinorhizienne *Gymnostoma papuanum*. La formation de racines regroupées chez le *G. papuanum* cultivé dans l'eau est influencée par la quantité de phosphore et la source d'azote. L'aération est un facteur critique; les boutures non-aérées forment moins de racines groupées que les boutures aérées. La déficience en phosphore est la seule déficience nutritive qui conduit à une augmentation des racines groupées. Les plantules cultivées sous des conditions de faible teneur (0,8 mg L^{-1}) ou d'absence en phosphore, réagissent en développant une forte proportion de racines groupées, sans qu'il y ait réduction globale dans la croissance racinaire sur une période de 6 semaines. La réaction obtenue en variant la teneur en phosphore est modifiée par l'addition d'azote sous des formes différentes. L'azote apporté sous forme d'ammonium réduit la quantité de racines groupées. L'apport de nitrate sur des plants nodulés conduit à une augmentation des racines groupées comparativement aux plantes qui dépendent seulement de la fixation de l'azote diatomique fixé par le *Frankia*. La plus forte formation de racines groupées apparait sur les plantes cultivées dans l'eau aérée additionnée de nitrate et avec de petites quantités ou pas du tout de phosphore.

Mots clés : *Gymnostoma papuanum*, racines groupées, racines protéoïdes, déficience en phosphore.

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Introduction

In describing the morphology of roots of some species from the family Proteaceae, Purnell (1960) defined a "proteoid root" as a "cluster of rootlets, of limited growth, which forms on a lateral root." Proteoid roots are commonly found on a majority of species in the Proteaceae (Lamont 1983), and factors that influence their formation have been extensively examined (Lamont 1972*a*, 1972*b*, 1973, 1976; Lamont and McComb 1974; Malajczuk and Bowen 1974; Lamont *et al.* 1984). In 1982, Lamont introduced the use of the general term "root clusters," which he defined as bunches of hairy rootlets produced on occasion by certain species and including proteoid and proteoid-like roots. We prefer to substitute the term cluster root for the more specific term proteoid root.

Cluster roots have been described for a number of species from families other than the Proteaceae. These plants include the legumes *Lupinus consentinii* (Trinick 1977), *Lupinus albus* (Gardner *et al.* 1981), and *Viminaria juncea* (Lamont 1972*c*), and the actinorhizal plants *Casuarina* spp. (Redell 1986) and *Myrica cerifera* (Louis *et al.* 1990). Phosphorus (P) in the root environment is an important factor in the production of cluster roots in several of these non-Proteaceae species. Trinick (1977) observed a decrease in their formation on *L. consentinii* with increasing P level, and Walker and Pate (1986) reported the same for *V. juncea*. Similarly, cluster root formation on *L. albus* is influenced predominantly by the P status of the plant (Gardner *et al.* 1982*b*). For *M. cerifera*, levels of P as low as 1 mg L^{-1} suppress the formation of cluster roots in hydroponics (Louis *et al.* 1990).

Gymnostoma papuanum (S. Moore) L. Johnson, an actinorhizal tree species in the family Casuarinaceae, falls within the category of plants that bear cluster roots. Cluster roots occur on hydroponically, aeroponically, and pot-grown plants in the greenhouse at Harvard Forest in Petersham. This study shows the effects of aeration, P supply, and nitrogen (N) source on cluster root formation on hydroponically grown *G. papuanum*.

Materials and methods

The following experiments on cluster root formation by *G. papuanum* were carried out in water culture using modified Hoagland's nutrient solution as specified for each experiment. At the time that experiment 1 was initiated, seed of *G. papuanum* was not available, therefore rooted cuttings were utilized. Seeds were later obtained and seedlings were then used for experiments 2–4. For all experiments,

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the harvest of each plant included counting the number of cluster roots and nodules (when present) and then separating shoot, nonclustered roots, cluster roots, and nodules, drying them for 2 days at 70°C, and then determining dry weights. Data were analysed with the assistance of the statistical software ABstat© (Anderson-Bell, Canon Bell, Colorado City, CO).

Experiment 1

Experiment 1 examined the effects of aeration and varying P levels on cluster root formation. Adventitious roots were induced on cuttings of *G. papuanum* according to procedures of Lundquist and Torrey (1984). Rooted cuttings were transferred to water culture jars (three per jar) and placed in a temperate-environment greenhouse. Each jar contained 1 L of quarter-strength Hoagland's nutrient solution, −N, pH 7.0 (Hoagland and Arnon 1950). All plants were inoculated with *Frankia* isolate HFPGpI1 (Racette and Torrey 1989). When nodules had been initiated on over 50% of the plants (4 weeks), the nutrient solution was replaced with treatment solutions (six jars per treatment), and half of the jars of each treatment were aerated using an aquarium pump and plastic tubing. Treatment solutions consisted of quarter-strength Hoagland's, −N, pH 7.0, with various P levels. P levels were selected based on the amount of P normally in quarter-strength Hoagland's (8 mg l^{-1}). The four P levels used were 16, 8, 0.8, and 0 mg L^{-1}. At 16 mg L^{-1} P, additional P was supplied as NaH_2PO_4 and at 0 and 0.8 mg L^{-1} P, KCL replaced the KH_2PO_4, which was eliminated. Nutrient solutions were changed every 2 weeks. Plants were harvested 15 weeks after treatments began.

Experiment 2

Experiment 2 tested the effect of using different N sources and P levels on cluster root formation. Seedlings of *G. papuanum* were established from seed collected at the Waiakea Arboretum in Hawaii using procedures described by Racette and Torrey (1989). Seedlings were placed in 0.5-L water culture jars, three plants per jar. All jars were placed in a growth chamber on a 16 h light : 8 h dark cycle at 33:28°C (light:dark), and all were aerated. For this and following experiments, the formulations of Hoagland's nutrient solutions used were based on Machlis and Torrey (1956), made up at quarter-strength. Treatments consisted of varying P levels and N sources. P levels used were the same as in experiment 1. For each P level, three jars received quarter-strength Hoagland's nutrient solution with NO_3^-, three jars received an NH_4^+-containing solution, and plants in three jars were inoculated with *Frankia* isolate UFGCeI5 (kindly provided by H. Berg) and received a −N nutrient solution. For the NH_4^+ treatment, $(NH_4)_2SO_4$ was substituted for NO_3^- at a level that supplied a N molarity equivalent to the NO_3^--containing solution (3.75 mM). Solutions were replaced once, after 4 weeks, and plants were harvested after 6 weeks. Nine plants were started for each treatment, but only six from each treatment were harvested because of seedling death during the experiment.

Experiment 3

Experiment 3 examined cluster root formation of nodulated seedlings growing at different P levels, either with or without added nitrate. Seedlings were set up in 0.5-L water culture jars containing quarter-stength Hoagland's nutrient solution, −N, 0.8 mg L^{-1} P, pH 7.0, and inoculated with *Frankia* isolate UFGCeI5. All jars were placed in the greenhouse and aerated. Solutions were changed after 4 weeks and after 6 weeks were replaced with treatment solutions, three jars per treatment. Nodulation was confirmed on all plants before treatments were started, and formation of cluster roots had begun on some plants. Treatments consisted of quarter-strength Hoagland's solution modified to contain three P levels (8, 0.8, and 0 mg L^{-1}) in combination with two N treatments (± NO_3^-). Solutions were changed after 2 and 4 weeks of treatment, and plants were harvested 6 weeks after treatments began (eight plants per treatment). An acetylene reduction assay (Burris 1974) was used to determine the degree of suppression of nitrogenase activity due to the addition of nitrate to the nutrient solution. Immediately prior to harvest, individual plants were incubated in 10% acetylene for approximately 1 h, and the amount of ethylene produced was measured on a Carle 9500 flame ionization gas chromatograph.

FIG. 1. Cluster roots on *G. papuanum* grown in water culture. Scale bar = 5 mm.

Experiment 4

Experiment 4 tested the effects of a range of nutrient deficiencies on cluster root formation. Seedlings were placed in 0.5-L jars containing the following modified quarter-strength Hoagland's solutions: −S, −Mg, −K, −Fe, −Ca, −P, −N, and − trace elements (formulations based on Machlis and Torrey 1956). Hoagland's complete nutrient solution at quarter-strength was run as a control, and all solutions were adjusted to pH 7.0 prior to use. Nine seedlings (three jars) were set up for each treatment. All jars were placed in a growth chamber and aerated (as for experiment 2). Solutions were changed after 2 and 4 weeks, and plants were harvested after 6 weeks.

Results

Gymnostoma papuanum spontaneously produced cluster roots after a period of time when grown hydroponically in quarter-strength Hoagland's nutrient solution. Clusters averaged 3.3 ± 1.4 mm in length, with 12.4 ± 1.7 rootlets per mm, and individual rootlets were generally 3 mm or less in length (Fig. 1). As the following results indicate, cluster root formation can be increased or decreased by manipulation of culture conditions, specifically aeration and nutrient supply.

Experiment 1

In experiment 1, the increase in cluster root formation by plants grown with aeration compared with plants grown without aeration was highly significant ($p < 0.01$). The amount of cluster root formation increased on a per plant basis, and a

TABLE 1. Growth and cluster root development of rooted cuttings of *G. papuanum* grown for 15 weeks at different phosphorus levels in water culture, with or without aeration (expt. 1)

	Phosphorus level (mg L^{-1})			
	0	0.8	8.0	16.0
No. of plants with clusters				
Nonaerated	4	2	2	4
Aerated	7	6	5	7
% of plants with clusters				
Nonaerated	57	29	29	57
Aerated	100	86	71	100
Shoot dry weight				
Nonaerated	270 ± 40	233 ± 30	219 ± 53	178 ± 28
Aerated	185 ± 45	284 ± 40	189 ± 42	244 ± 40
Total root dry weight				
Nonaerated	79 ± 9	59 ± 7	74 ± 18	63 ± 10
Aerated	58 ± 15	77 ± 13	103 ± 60	62 ± 10

NOTE: Shoot and root dry weights (mg/plant, $\bar{X}$ ± SE) were not significantly different owing to either aeration or P level.

greater number of plants formed cluster roots with aeration (Table 1). Increased cluster root formation was not due to an increase in plant growth, as there was no significant difference in root or shoot dry weights as a result of either aeration or P level (Table 1). The graphs in Fig. 2 suggest that in aerated cultures, cluster root formation increased as P level decreased, although there was no statistically significant difference in cluster root number, in cluster root dry weight, or in the percentage of the total root weight made up of cluster roots due to the change in P level. Lack of statistical significance may be attributable to the high within-treatment variation that occurred despite the use of clonal plants.

Experiment 2

In experiment 2, both P level and N source had highly significant effects ($p < 0.01$) on the formation of cluster roots on seedlings (Fig. 3). In general, decreasing P level led to increased cluster root development regardless of the N source, but this effect was most pronounced when NO_3^- was supplied. Although plants grew best when NH_4^+ was the N source (Table 2), cluster root formation was eliminated at 8 and 16 mg L^{-1} P and much reduced at the lower P levels compared with NO_3^--fed plants. For inoculated plants, development of cluster roots did not show as much variation with changing P level as it did for plants given fertilizer N. The inoculated plants did not nodulate until 3 weeks into the experiment, and as a result, nodulated plants were significantly smaller at the end of the experiment than in either NO_3^--or NH_4^+-fed plants (Table 2). Whether this affected cluster root development could not be determined, but there did not appear to be any significant lag time in the onset of cluster root development between N treatments. In relation to root growth, although decreasing P level led to increased cluster root formation, there was no significant change in total root weight due to the change in P supply. This result indicates that the decrease in P resulted in a change in the type of root growth occurring, not in the total amount of root growth.

Experiment 3

Experiment 3 was designed to determine whether the reduction in cluster root formation on inoculated versus NO_3^--fed plants in experiment 2 would remain if all plants were first inoculated. The plan was to eliminate from the experimental period the N-free time that occurred during the nodulation process and thereby equalize growth among treatments. Results in Table 3 suggest that this effect was accomplished, as there was no significant difference in root or shoot dry weights owing to N treatments. The addition of NO_3^- to nodulated seedlings did result in a decrease in final nodule number and nodule dry weight per plant, as well as a significant decrease in nitrogenase activity, both per gram of nodule dry weight and per plant, but did not lead to an increase in plant growth. Although all plants grew equally well, the graphs in Fig. 4 clearly indicate that plants supplied with NO_3^- formed significantly more cluster roots in comparison with those which depended on N_2 fixed by *Frankia*. The relation between P level and cluster root formation is not as clear as in experiment 2, but there was still a significant increase in cluster root dry weight and the percentage of root expressed as cluster roots at the 0 P level ($p < 0.05$). The lack of more significant variation in relation to P level may relate to the 6-week pretreatment period in which all plants received 0.8 mg L^{-1} P.

Experiment 4

In this experiment, cluster root formation was significantly greater on plants grown in a solution lacking P, compared with all other treatments (Duncan's multiple range test, $p < 0.01$), as measured by cluster root dry weight and by the percentage of the total root weight made up of cluster roots (Fig. 5). Cluster roots that formed in −P were generally larger than clusters in other treatments, with each cluster having more rootlets. The number of cluster roots varied tremendously among plants for some treatments, including the control where with a mean of 13.7 clusters per plant, there was a range of 0–76 clusters per plant, resulting in a standard deviation of 24.2. While the highest mean number of cluster roots per plant occurred with −P (26.3), the large within-treatment variation resulted in no significant difference in cluster root numbers among the control, −P, −Ca, and −Mg treatments.

Discussion

The formation of cluster roots by *G. papuanum* grown in water culture is highly dependent on growing conditions and nutrient supply. Three factors, P supply, aeration, and N source, markedly influence the amount of cluster root formation that occurs. Each of these factors will be discussed in turn.

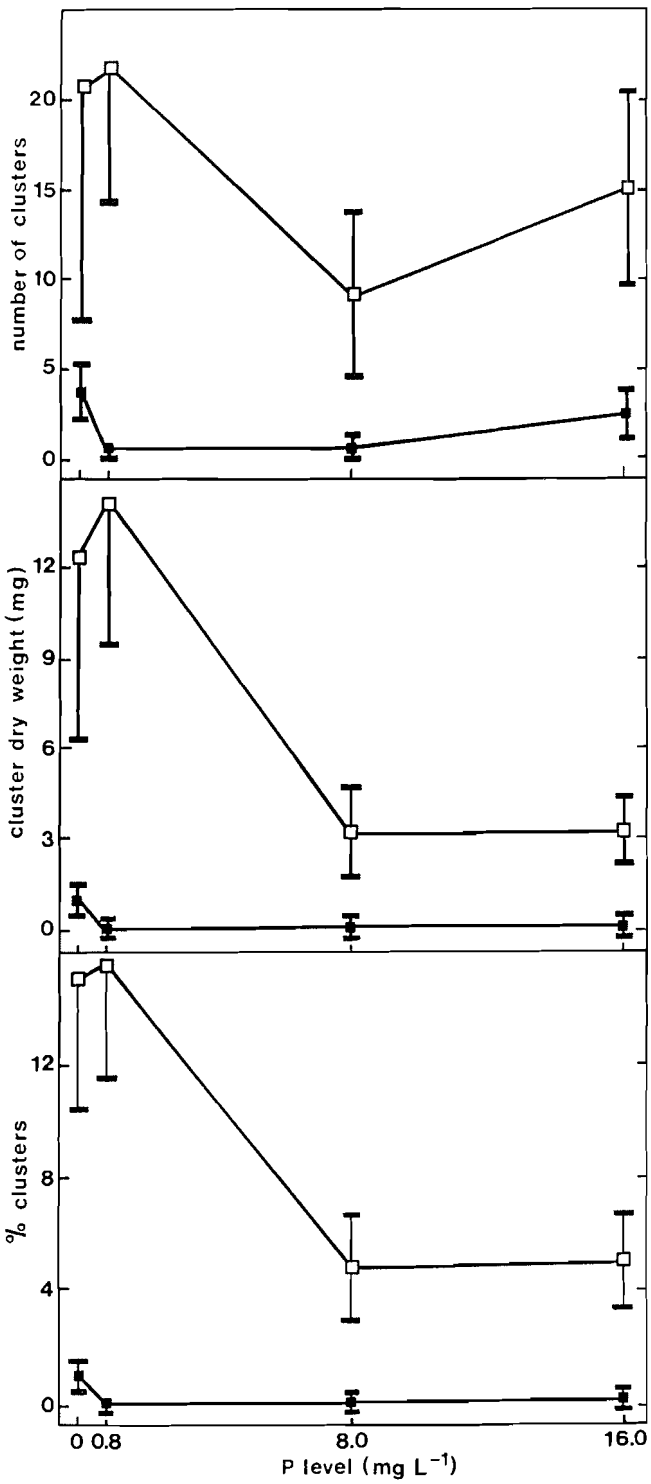

FIG. 2. Cluster root formation by aerated (□) and nonaerated (■) rooted cuttings of *G. papuanum* grown in water culture for 15 weeks at four levels of P (expt. 1). Vertical lines represent ±SE. Top: number of cluster roots per plant. Middle: cluster root dry weight per plant. Bottom: percentage of total root consisting of cluster roots, based on dry weights.

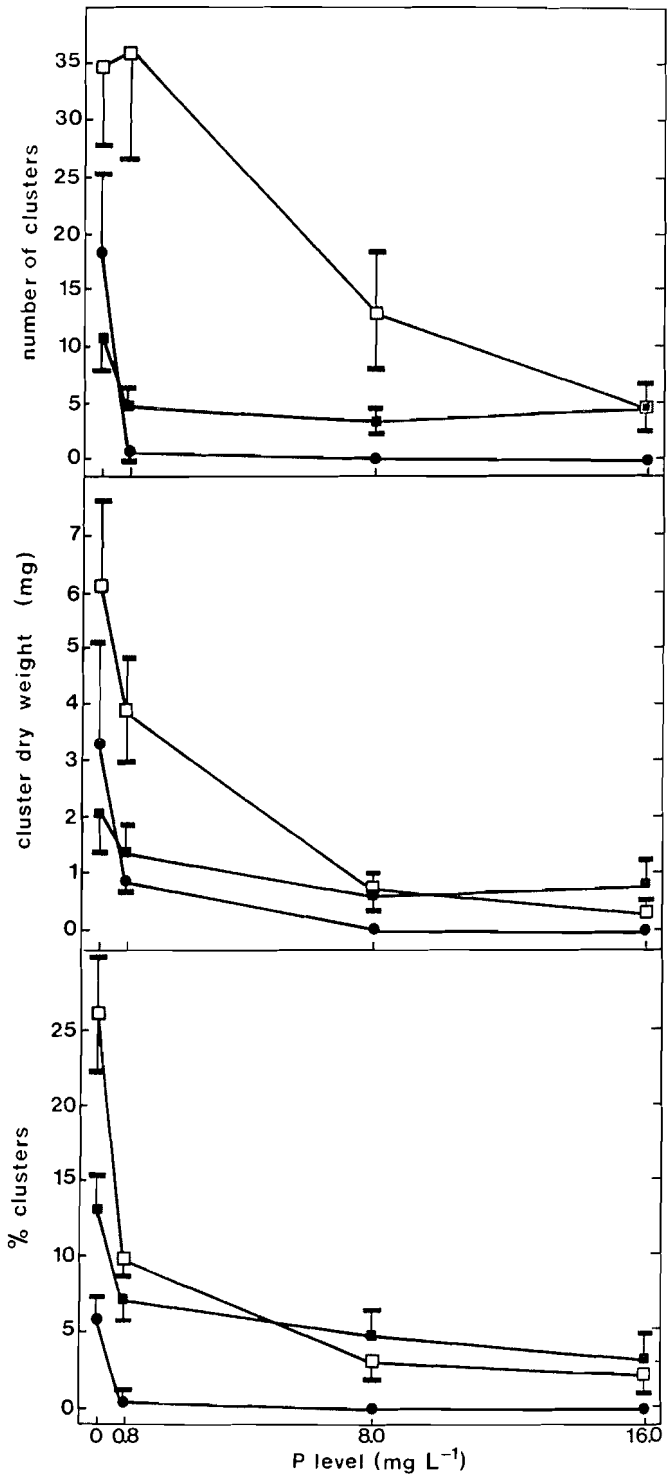

FIG. 3. Cluster root formation by seedlings of *G. papuanum* grown for 6 weeks at four P levels with three different nitrogen sources (expt. 2). Nitrogen was provided as ammonium (●), nitrate (□) , or dinitrogen fixation by *Frankia* (■). Vertical lines represent ±SE. Top: number of cluster roots per plant. Middle: cluster root dry weight per plant. Bottom: percentage of total root consisting of cluster roots, based on dry weights.

While the results of the nutrient-deficiency experiment do not rule out an influence of other nutrients, only when P was the missing nutrient was there a significant increase in cluster root formation. *Gymnostoma papuanum* responds to a deficiency of P by devoting a greater portion of root growth to the formation of cluster roots. This observation fits the hypothesis of Jeffrey (1967) that proteoid roots form as a response to the low-P status of plants. Increase in cluster root formation due to decreasing P availability has been clearly shown for several

TABLE 2. Comparison of different nitrogen sources and phosphorus levels on shoot and root growth of *G. papuanum* seedlings after 6 weeks of treatment (expt. 2)

	Phosphorus level (mg L^{-1})			
	0	0.8	8.0	16.0
Shoot dry weight				
NO_3^-	90 ± 14	188 ± 34	115 ± 21	76 ± 17
N_2	56 ± 11	61 ± 16	54 ± 16	72 ± 23
NH_4^+	159 ± 49	186 ± 41	218 ± 42	163 ± 41
Total root dry weight				
NO_3^-	22 ± 4	38 ± 6	22 ± 3	18 ± 5
N_2	15 ± 4	16 ± 4	10 ± 3	16 ± 5
NH_4^+	47 ± 14	45 ± 9	37 ± 7	39 ± 13

NOTE: Values in table are expressed as mg/plant ($\bar{x}$ ± SE). Significant differences were due to N source ($p < 0.01$), but no significant difference was due to P level. N_2 is fixed nitrogen provided via biological N_2 fixation by *Frankia*.

TABLE 3. The effects on nodulation, nitrogenase activity, and growth of supplying NO_3^--containing nutrient solution and varying P to nodulated *G. papuanum* seedlings after 6 weeks of treatment (expt. 3)

	Phosphorus level (mg L^{-1})		
	0	0.8	8.0
Shoot dry weight*			
No nitrate	81 ± 9	72 ± 13	83 ± 13
Nitrate	73 ± 12	97 ± 16	54 ± 5
Total root dry weight*			
No nitrate	32 ± 4	26 ± 5	26 ± 4
Nitrate	27 ± 4	35 ± 6	19 ± 3
No. of nodules/plant†			
No nitrate	41 ± 7	34 ± 5	30 ± 4
Nitrate	25 ± 4	31 ± 3	21 ± 3
Nodule dry weight†			
No nitrate	8.1 ± 1.4	7.5 ± 1.6	7.8 ± 1.4
Nitrate	2.3 ± 0.3	2.7 ± 0.3	2.0 ± 0.2
Acetylene reduction			
Per plant†			
No nitrate	0.11 ± 0.01	0.10 ± 0.02	0.17 ± 0.03
Nitrate	0.01 ± 0.003	0.03 ± 0.01	0.01 ± 0.002
Per nodule†			
No nitrate	14.1 ± 1.4	14.0 ± 1.4	21.1 ± 2.2
Nitrate	2.4 ± 1.3	9.0 ± 2.4	2.9 ± 0.7

NOTE: Values in table are means ± SE. Shoot dry weight, root dry weight, and nodule dry weight were measured as mg/plant. Acetylene reduction per plant was measured as μmol C_2H_4/(plant·h) and per nodule as μmol C_2H_4/(g nodule dry wt·h).

*No significant differences due to NO_3^- treatment or P level.

†Significant differences due to NO_3^- treatment ($p < 0.05$), but no significant differences due to P level.

species other than *G. papuanum*, but the response is somewhat variable. A second actinorhizal plant for which the response to P has been studied is *M. cerifera* (Louis *et al.* 1990). *Myrica cerifera* forms cluster roots at very low P levels, with as little as 1 mg L^{-1} P in the nutrient solution of hydroponically grown plants totally suppressing cluster root formation. In contrast, *G. papuanum* continues to form cluster roots at 16 mg L^{-1} P, more closely resembling cluster root formation of the legumes *V. juncea* (Walker and Pate 1986) and *L. albus* (Gardner *et al.* 1982*b*), which show decreasing cluster root formation with increasing P fertilization but still form some cluster roots when a moderate level of P is present. Despite this continued formation of cluster roots at higher P levels, seedlings of *G. papuanum* grown in water culture appear to have a very low requirement for P, with no reduction in growth occurring even at 0.8 mg L^{-1} P (= 1/10 of quarter-strength Hoagland's nutrient solution). It is probable that the difference between *M. cerifera* and *G. papuanum* is therefore not related to the absolute requirement of each species for P but rather to the metabolic response of each species to varying internal P status. Cluster root formation appears to be a more tightly regulated phenomenon for *M. cerifera*.

Although the level of P supplied in the nutrient solution had an important influence on the type of root growth that *G. papuanum* expressed, it appeared to have little significance in relation to total plant growth over the length of time that these experiments were run. In experiment 1, rooted cuttings that did not receive P for 15 weeks showed no significant reduction in growth in comparison with plants receiving P. Likewise, in experiments 2–4, seedlings grown for 6 weeks with no externally supplied P grew as well as seedlings receiving P in the nutrient solution. While *G. papuanum* is relatively slow growing, significant growth did occur during all experiments. These results suggest that both seedlings and rooted cuttings of *G. papuanum* require only low amounts of P for growth, and the plants are able to provide the necessary amount of P from

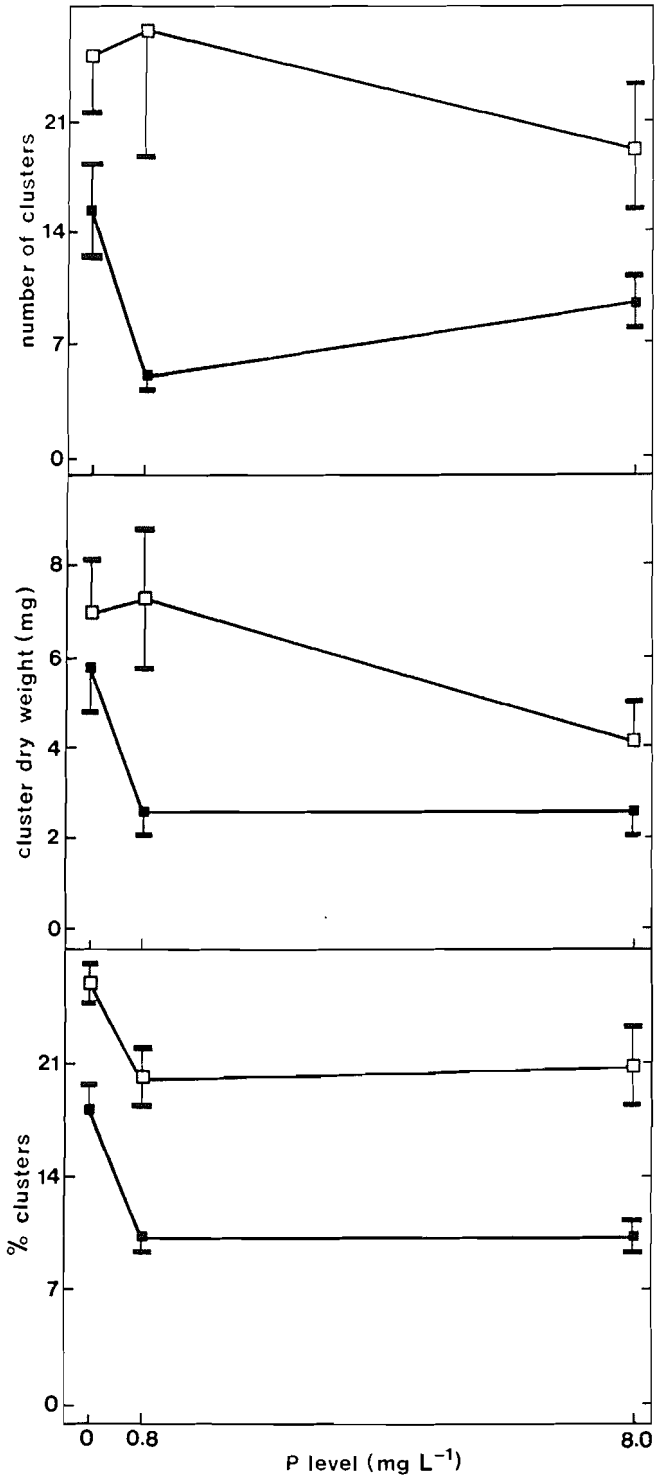

FIG. 4. Cluster root formation on nodulated seedling of *G. papuanum* with (□) or without (■) nitrate (expt. 3). Plants were grown at three P levels and received nitrate treatment for 6 weeks, subsequent to a 6-week period for nodulation during which all plants received 0.8 mg L^{-1} P. Vertical lines represent ± SE. Top: number of cluster roots per plant. Middle: cluster root dry weight per plant. Bottom: percentage of total root consisting of cluster roots, based on dry weights.

internal reserves for extended periods of time when external supplies are limited. Thus, abundant cluster root formation may serve as an indicator of low external P supply when growth-related P deficiency symptoms are not evident in *G. papuanum*.

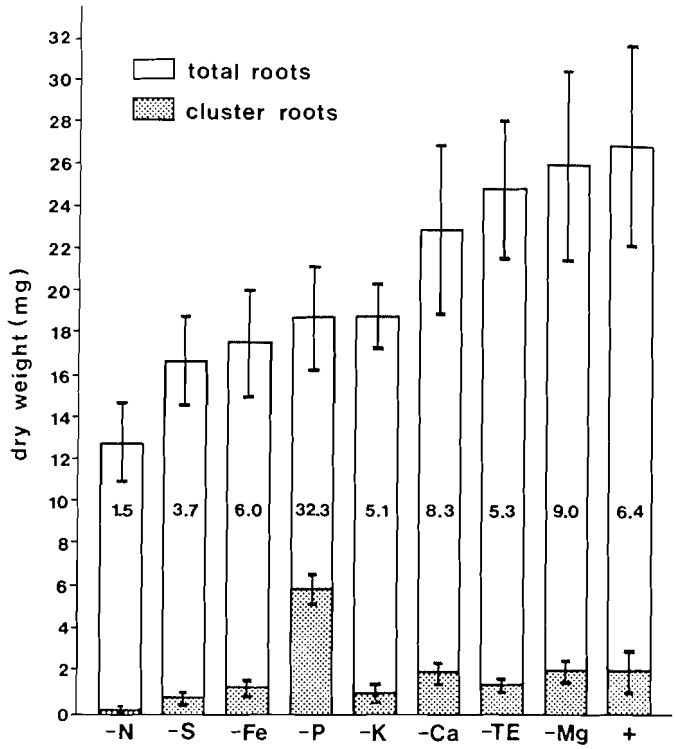

FIG. 5. Total root dry weight and dry weight of cluster roots formed on seedlings of *G. papuanum* grown in water-culture solutions deficient in mineral nutrients as noted. TE, trace element; +, complete nutrient solution. Numbers within bars are the percentages of total root weight consisting of cluster roots. Vertical lines represent ± SE.

The effects of aeration on cluster root formation were statistically highly significant, with an increase in both the number of plants that formed cluster roots and the amount of cluster root formation per plant when cultures were aerated. The dramatic increase that occurred does not appear to be directly related to growth rate, as nonaerated plants were on average the same size as aerated ones. This fact suggests that there may be an additional requirement of the root for air (oxygen) to form cluster roots beyond that required for normal growth and maintenance. The formation of cluster roots involves a large amount of meristematic activity and cell growth, and presumably, therefore, a high respiration rate within localized short segments of root. It is possible that the need for aeration thus relates to a higher demand for oxygen at the time and sites of cluster root development. These results correlate well with the observations of Lamont (1976) who showed that maximum proteoid root numbers on *Hakea* occurred under conditions of moderate waterlogging, decreasing if water availability increased (oxygen decreased).

Lamont (1972*a*) reported that of the factors studied, N concentration appeared to have the greatest effect on determining the relative contribution of proteoid roots to the root system of *Hakea*. Later, Lamont (1973) demonstrated that proteoid root production was decreased by an increase in N status of shoots of *Hakea* plants. Since *G. papuanum* forms a symbiotic relationship with the dinitrogen-fixing bacterium *Frankia*, the relationship of N to cluster root formation is particularly interesting. In our experiments, the effect of three different sources of N was examined. The results indicate that the source of N influences the formation of cluster roots to a significant degree.

Ammonium was the best source of N for growth, but its use led to the lowest level of cluster root production. If, in this case, the greater growth of ammonium-fed plants indicates a higher shoot N status, then these data agree with the results of Lamont's work. The difference between plants receiving nitrate N and those growing solely with dinitrogen fixed by *Frankia* is not as clear. These plants appeared to grow equally well, but those receiving nitrate produced significantly more root clusters. Further experiments using different levels of N and determining actual shoot and root N content will be necessary to better understand the relationship between N source and cluster root formation. Furthermore, the relationship between N source and cluster root formation may not be the same for other species. A similar experiment with *M. cerifera* showed no difference in cluster root formation between plants that did or did not receive a nitrate-containing nutrient solution (Louis *et al.* 1990).

While it is clear that both P and N nutrition are involved in the regulation of cluster root formation, the mechanism whereby this developmental expression occurs is not obvious. The ultimate basis for the control of cluster root formation must lie in the effects of these nutrients on factors that regulate the initiation of new lateral root meristems, including the levels of hormones such as auxin (cf. Torrey 1986). For those plants which form them, cluster roots may actually be the normal type of root growth found in the field, where P levels are often very low, and their occurrence may be much more widespread than currently reported. Of course, this leads to the question of whether or not the formation of cluster roots at low P levels is of benefit to the plant. Work on *L. albus* (Gardner *et al.* 1981, 1982*a*, 1982*b*, 1983) does suggest a possible mechanism whereby cluster roots may allow for increased P uptake by a plant. Further work with other plants that form cluster roots, perhaps including *G. papuanum*, will be necessary before the question of function is resolved.

Acknowledgements

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