

## CARBON AND NITROGEN FIXATION IN RHIZOMATOUS SPECIES OF *CORIARIA*

G. T. DALY, B. E. SMITH AND SIEW CHUA

*Lincoln College, Canterbury*

**SUMMARY:** The rhizomatous species *Coriaria sarmentosa* and *C. angustissima* bear coralloid clusters of root nodules which actively fix atmospheric nitrogen. Using rooted cuttings, comparative measurements were made of growth, net photosynthesis, dark respiration and nitrogen fixation in the two species. In both, the optimum temperatures for growth and net photosynthesis are 16-18°C. Over a range of temperature and light intensity *C. sarmentosa* possesses a higher rate of net photosynthesis than its more diminutive sister species *C. angustissima*. When grown in soil collected beneath rhizomatous *Coriaria* in the field, nodulated *C. sarmentosa* responded significantly to sulphur and phosphorus when added together. The acetylene reduction method was used to measure rates of nitrogen fixation in excised modules of both species in various environmental conditions. Nitrogenase activity appears most vigorous in *C. sarmentosa* nodules at temperatures approaching 22°C. Rates of acetylene reduction appear to be similar in both species but vary according to clone and pre-treatment temperature. Nodule efficiency is higher in young nodules than in old and compares favourably with those reported for other nodulated nitrogen fixers. These results tend to confirm some of our earlier assumptions about the ecology of these successional species. Though considered as weeds on grazing land they may have a place in planting programmes for erosion control in wet scree country.

### INTRODUCTION

Species of *Coriaria* are botanically notable for several reasons, the most distinctive being possession of nitrogen-fixing root nodules. Monogeneric, the family Coriariaceae has an extremely discontinuous world distribution. One or more species are endemic to New Zealand, Kermadec Islands, Chile, Japan, Himalayas and Spain. Much attention has been focused on such nodulated non-legumes and their significance in the pioneer stages of plant succession and soil development (e.g. Becking 1970, Bond 1967, Stewart 1968). Reports from Japan, Spain and Chile indicate the ecological similarity of other members of the family to the seven species of New Zealand tutu. But the native tutus are also poisonous and are considered to be noxious weeds. In hill country pastures patches of toxic tutu have caused losses in stock unwary enough to browse the luxuriant flowers and foliage.

Recent work has provided a wealth of information on one species, *C. arborea* (Silvester 1968) and a little about several others (Burke 1963). A lot more is needed on the rhizomatous tutu. Mr L. D. Bascand in Otago is studying *C. sarmentosa*

as an agricultural weed. He is emphasising chemical and ecological techniques designed to eradicate the species from grazing lands. The task of eradicating rhizomatous, frost-tender species of *Coriaria* from pastures is made easier by the very low viability of their seeds.

This paper reports part of a project on the ecological physiology of *C. sarmentosa* (grassland tutu) and *C. angustissima* (sub-alpine tutu). We are interested in the possibility of making use of the cold-tolerant growth habit and nitrogen fixation of these creeping plants. Both take part in pioneer vegetation of moist gravels, silts and disturbed soil throughout montane and sub-alpine climates of the South Island. It would be useful to test the feasibility of using these rhizome-forming, native nitrogen fixers in the revegetation of eroding forest and scrublands. Throughout both Islands there are areas where the grazing of domestic stock is not part of the land-use, e.g. National Parks, Forest Parks, unoccupied Crown Lands, road verges and Water Reserves. Eroding catchments within such land are ideally suited to the encouragement of plant successions including native tutu. An example of such a succession is given in Figure

1 which shows a rhizomatous mat of *Coriaria* spreading over lateral moraine of the Mueller Glacier, Mt Cook.

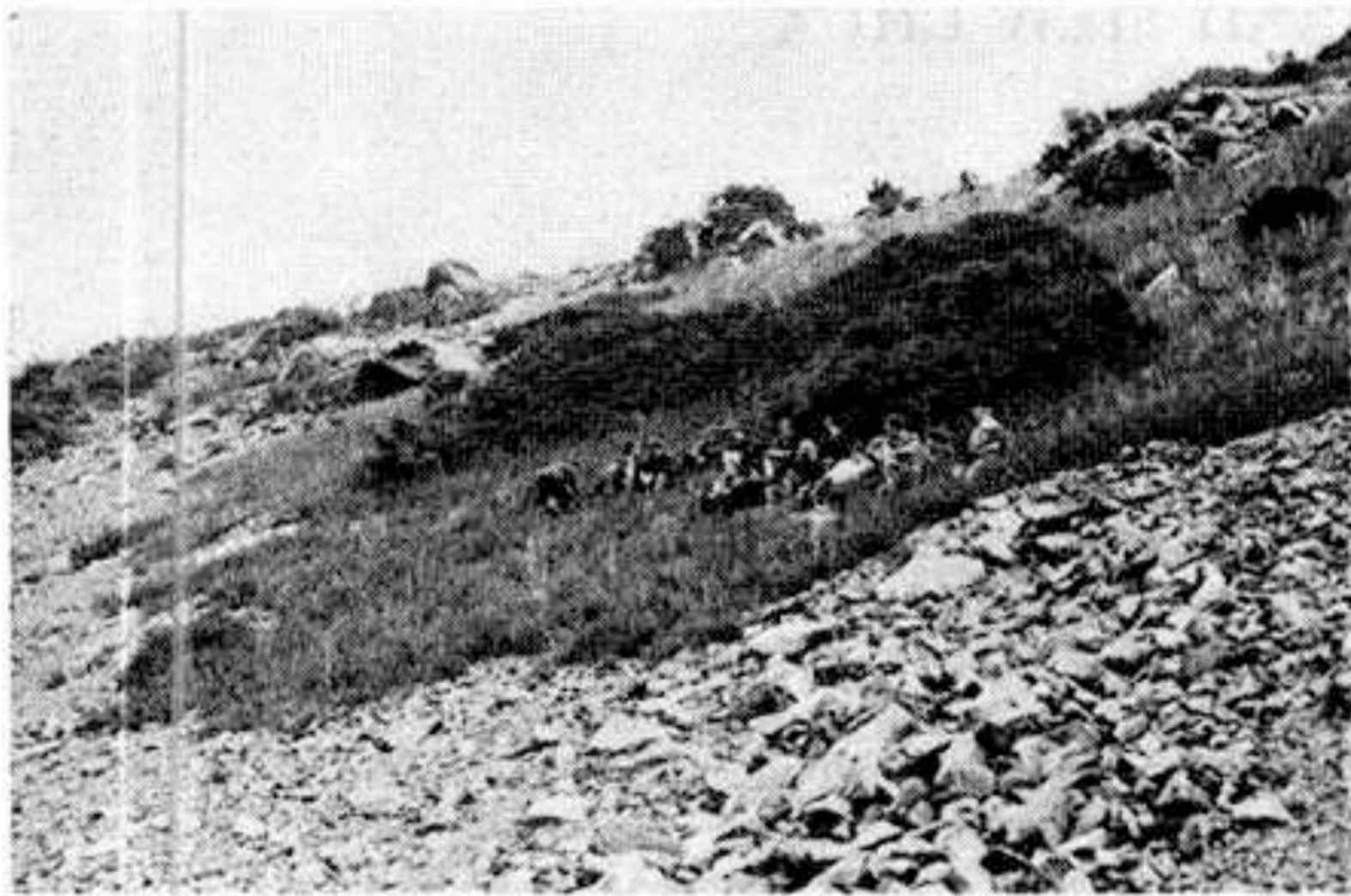


FIGURE 1. *Coriaria* colonising unstable moraine gravel, Mueller Glacier, Mt Cook. Note the large shrubs of *Podocarpus nivalis* behind the group of students.

#### GROWTH IN CONTROLLED ENVIRONMENT

##### *Methods and Materials*

Measurement of the species in controlled conditions complements field observations of altitudinal range and ecological position. Vegetative growth, carbon and nitrogen fixation and response to soil fertiliser have been measured in four clones of both *C. sarmentosa* and *C. angustissima*. These clones were raised from near even-sized cuttings taken from crown and rhizome stems. Because of poor seed germination, seedlings are, at present, difficult to obtain in sufficient numbers for factorial pot experiments.

Brought into cultivation in Spring 1968, the clones were rooted in trays of soil collected within *Coriaria* colonies in the field. Root nodulation was vigorous and occurred in all plants of each clone. After three months growth all cuttings of both species were potted reciprocally into their native soils. Washed river sand at the rate of 25 per cent by weight was mixed with both soils to improve pot drainage. A further three months followed in hot, well-watered glasshouse conditions. All vigorous cuttings were then grouped, treated with the appropriate fertiliser combination and placed in

the growth cabinets. Position of each pot in the cabinets was established by random numbers. At the time of transfer to cabinets and application of sulphur and phosphorous fertiliser the average dry weight per plant was 2.8g for *C. sarmentosa* and 0.6g for *C. angustissima*.

Each cabinet was 1.7 metres long x 1.5m high. They were illuminated by 48, 80W, fluorescent tubes and 18, 60W, incandescent strip-lights. Day-length was controlled by a time-clock. Air was circulated upwards through the plant shelf by a fan.

Temperature was maintained at set point  $\pm 1^{\circ}\text{C}$  by a pneumatic controller which modulated a valve on the glycol-filled ( $-5^{\circ}\text{C}$ ) heat exchanger for cooling and switched a tubular heater on for heating. In each cabinet temperature was measured by thermocouples and recorded on a multi-channel potentiometric strip chart recorder. Humidification was achieved by means of a humidistat-controlled water/air spray.

Ambient temperatures in the three artificially-lit cabinets were set at "high" ( $24^{\circ}\text{C}$  day and  $16^{\circ}\text{C}$  night), "medium" ( $18^{\circ}\text{C}$  day and  $10^{\circ}\text{C}$  night) and "low" ( $10^{\circ}\text{C}$  day and  $3^{\circ}\text{C}$  night). The average light intensity at plant level in each cabinet was measured as 22 K.lux, while day-length was set to 16 hours and relative humidity to 85 per cent. During 4.5 months growth in these relatively controlled environments one operating difficulty was only partly overcome. This was the tendency to give too much water to plants in the low temperature chamber while keeping pace with the high water consumption in the high temperature conditions.

##### *Results and Discussion*

###### *a. Growth at Different Temperatures*

All plants were harvested in July 1969 after 18 weeks exposure to the various treatments. Each plant was measured, stems counted and separated into leaves, stems, roots, nodules and original cutting. All tissues were then dried for several days to constant weight at  $85^{\circ}\text{C}$ , weighed oven-dry and stored for future chemical analysis.

Average dry weights per plant for both *C. angustissima* and *C. sarmentosa* are given in Table 1.

The dry weight data are grouped according to plant performance in three temperatures and two soils—a disturbed youthful profile in the Tekoa Y.B.C. zone collected in the Craigieburn River to Bealey area and a very young developing soil on glacial moraines, Mt Cook.

TABLE 1. *Response of Tutu to Temperature*  
(Average dry weight in grams per plant)

		Day/Night Temperature (°C) In Growth Cabinet		
		10/3 g.	18/10 g.	24/16 g.
<i>C. angustissima</i>	Disturbed Tekoa YBE	1.4	10.2	9.6
	Young glacial moraine, Mt Cook	3.2	10.0	6.7
<i>C. sarmentosa</i>	Disturbed Tekoa YBE	5.9	20.8	19.1
	Young glacial moraine, Mt Cook	8.6	20.7	19.3

For both species optimum temperatures for growth appear to be in the range provided by the medium temperature treatment. In addition, the inherent difference in plant size between the two species is maintained at the three temperatures. The only notable difference in performance in the two soils occurs at low temperature. Here the wet, cool conditions allowed expression of the superior drainage and root aeration of the young glacial moraine soil.

A visual impression of these differences is given in Figure 2. There are clearly differences too in leaf and stem coloration; plants of both species show bright brown to red pigmentation in low temperature. A feature of both species was the rapid leaf death and fall as soon as slight dehydration occurred. This phenomenon was noted in the high temperature cabinet and certainly contributed to the absence of a significant difference in dry weight between *Coriaria* plants from the high and moderate temperature conditions.

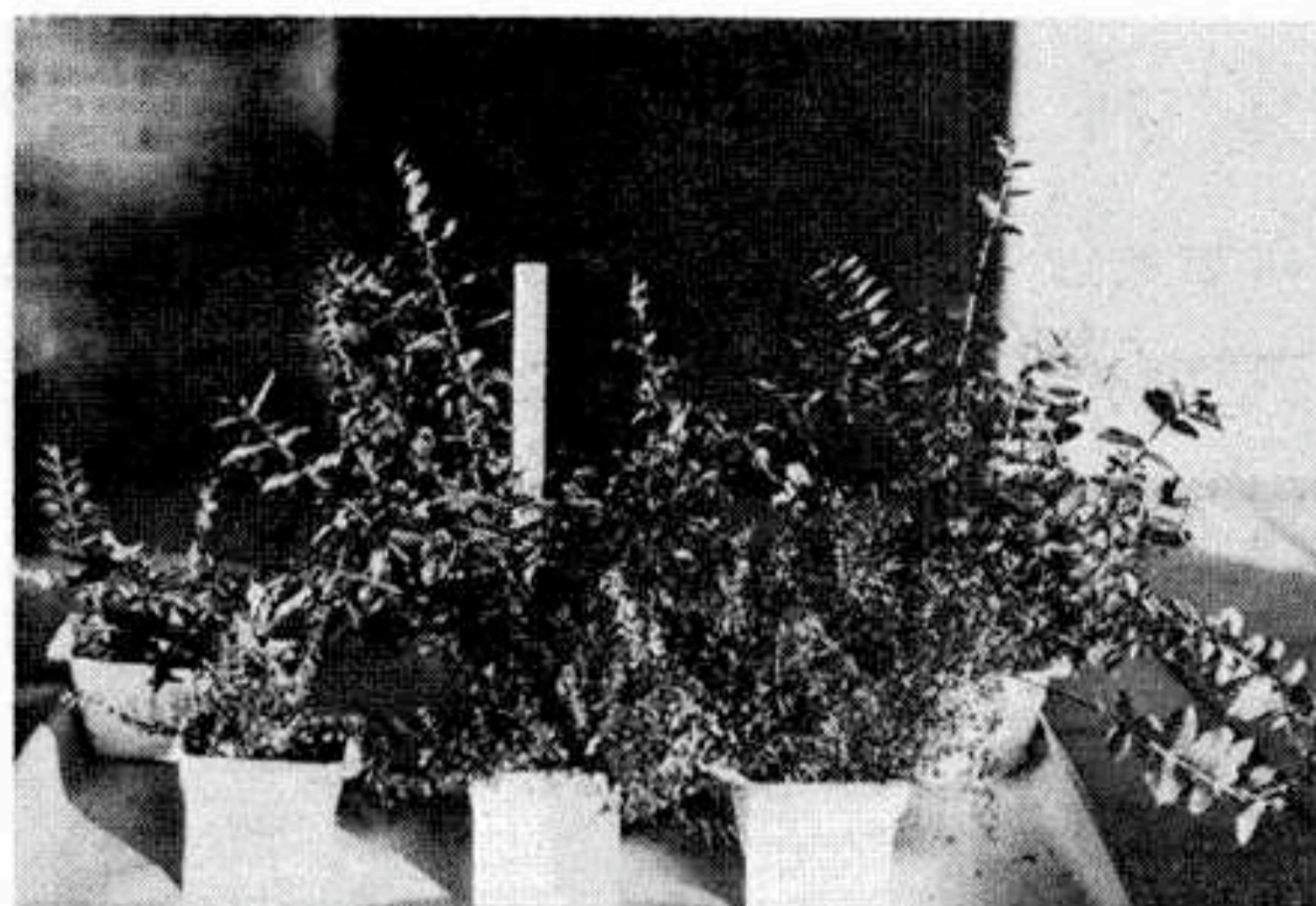


FIGURE 2. *Typical appearance of plants grown at three temperatures from cuttings taken from the two Coriaria species. C. angustissima, in the foreground, has leaves and stems noticeably smaller than those of C. sarmentosa. Temperature treatments: left to right, Low (LT), Medium (MT) and High (HT).*

#### b. *Response of C. sarmentosa to Sulphur and Phosphorus Fertiliser in Native Soils*

The growth cabinet experiment had a factorial design incorporating two species, four clones, two soils, three temperatures and two rates (some and none) of sulphur and phosphorus fertiliser. The effect of fertiliser tended to be similar for both soils. Complete fertiliser response data were obtained for *C. sarmentosa* only, because there were too few *C. angustissima* plants for complete factorial combinations. The typical visual difference between plants given both sulphur and phosphorus and those on unamended soils is shown in Figure 3. Table 2 sets out the average dry weight per plant in *C. sarmentosa* in both soils at all combinations of sulphur and phosphorus used. Sulphur was supplied as calcium sulphate equivalent to 100kg/ha and phosphate as 100 kg/ha of calcium dihydrogen phosphate.

There was a response to phosphorus alone and more clearly to sulphur alone. However, a well-defined positive interaction between phosphorus and sulphur is seen for *Coriaria* in both soils. This interaction is significant at the 1 per cent level. There is a remarkable similarity between this pattern of plant responses to added sulphur



FIGURE 3. Typical effect of addition of sulphur and phosphorus to *C. sarmentosa* growing in a disturbed upland yellow brown earth from inland Canterbury. Phosphate and sulphate equivalent to a rate of 200kg superphosphate/ha was applied to pot marked SP (right). Note the dark glossy foliage and vigorous shoot production of this plant compared with the pale leaves and suppressed appearance of control plant marked 00 (left).

TABLE 2. Response of *C. sarmentosa* to Sulphur and Phosphorus Amendment in Two Native Soils

(a) Disturbed Tekoa Y.B.E. From *C. sarmentosa* Sites in Inland Canterbury (Average D.W. per plant)

	P <sub>0</sub>	P <sub>100</sub>
S <sub>0</sub>	11.5	12.5
S <sub>100</sub>	15.5	21.7**

(b) Young Stony Silt From *C. angustissima* Sites Glacial Moraines, Mt Cook.

	P <sub>0</sub>	P <sub>100</sub>
S <sub>0</sub>	12.8	14.2
S <sub>100</sub>	16.7	21.4**

\*\*P<0.01.

and phosphorus and those obtained for nodulated legumes such as *Trifolium*, *Medicago* and *Lotus* species. This may be an example of the classical response by a symbiotic, nitrogen-fixing plant to the addition of sulphur and phosphorus to soils in which both these essential nutrients are in short supply. As would be expected in these young inland soils sulphur appears to be more limiting than does phosphorus (Walker

1965). These results indicate that in hill country yellow-brown earths *C. sarmentosa* as a weed might be expected to respond vigorously to aerially-spread superphosphate. It is also possible that sulphur fertiliser would assist nodulated *Coriaria* plants to become established on moist screes needing revegetation.

#### CARBON DIOXIDE EXCHANGE

##### Methods and Materials

In an effort to give more precision to information on ranges and optima for vegetative growth we carried out infra-red gas analysis (I.R.G.A.) of carbon dioxide exchange by leafy branches of both species.

Plants used in the I.R.G.A. were selected from the growth cabinet factorial experiment. Plants used were transferred from the three pre-treatment temperature cabinets to a fourth cabinet equipped for gas exchange measurements. Carbon dioxide exchange as net photosynthesis and dark respiration was analysed for a number of plants of both species from each pre-treatment at a range of leaf exposure temperatures and light intensities. Figure 4 shows the way in which three plants at a time, one from each pre-treatment temperature, were connected to the I.R.G.A. system.

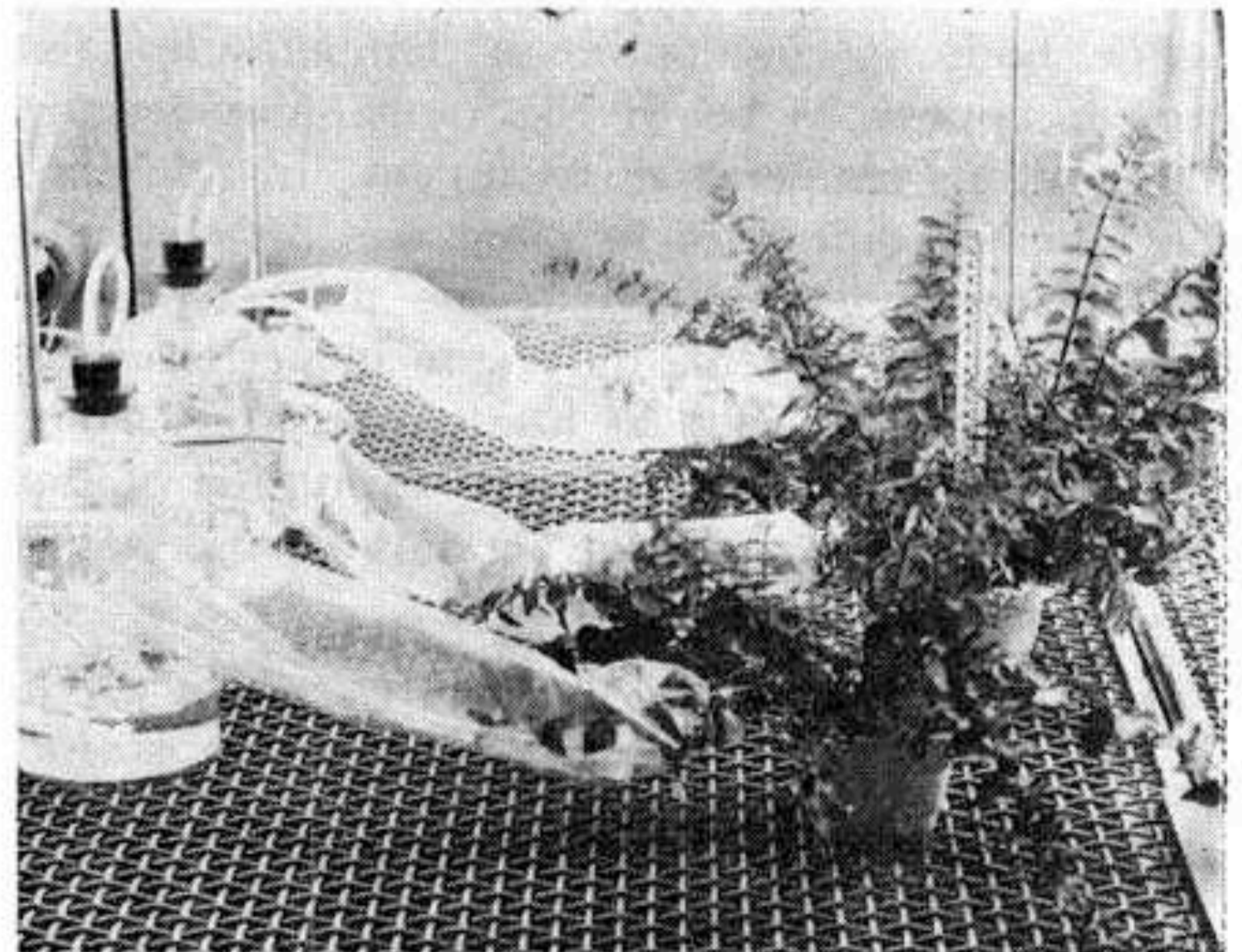


FIGURE 4. View of the growth cabinet in which carbon dioxide exchange measurements were made on *Coriaria* plants over a range of leaf temperatures and light intensities. Three plants at a time were connected to the gas stream by means of sealed polythene bags.

For infra-red gas analysis air was pumped from outside the building to a reservoir (mixing tank) and from this a tube was taken to the reference channel in the gas analyser—a Grubb Parsons model SB2. A tube was also taken from this reservoir, through a regulator and flowmeter “Gapmeter” via a humidifying chamber in the growth cabinet to the plant chamber.

The plant chamber consisted of a polythene envelope slightly larger than the stem and leaves of the plants to be measured, with an inlet tube sealed in one end and an exhaust tube sealed in the other. The open end of the chamber was sealed around the plant stem with a Hoffman screw clip. Clamping surfaces of this clip were covered with a strip of sponge rubber to aid the sealing of the plant chamber to the stem. This method was considered easier than using a silicone rubber impression medium as a seal because it allowed plants to be changed quickly and easily.

Using flow rates of 2-14 l/min the exhaust of the plant chamber was greater than that required by the analyser sample channel. Consequently excess was bled off to the atmosphere.

The reading on the meter of the analyser was proportional to the carbon dioxide differential between the sample and reference and was fed to a multi-channel potentiometric chart recorder. This recorder also controlled a sequential sampling system of three channels allowing the carbon dioxide exchange rates for three plants to be measured at the same time.

## Results and Discussion

### a. Net Photosynthesis and Dark Respiration at Different Temperatures

#### (i) *Coriaria sarmentosa*

The trends of net photosynthesis (PHS) at 20 K.lux light intensity and respiration at different leaf exposure temperatures are drawn in Figure 5. An optimum temperature for PHS in these clones of the species appears to be between 16 and 18°C. Dark respiration rates are not very high and tend to increase in a linear manner with temperature. At the time of measurement the dark respiration in mg CO<sub>2</sub>/dm<sup>2</sup> leaf/h

were obtained following photosynthesis at low temperatures. The low respiration figures might therefore be due more to low carbon substrate supply than to low genetically determined rates.

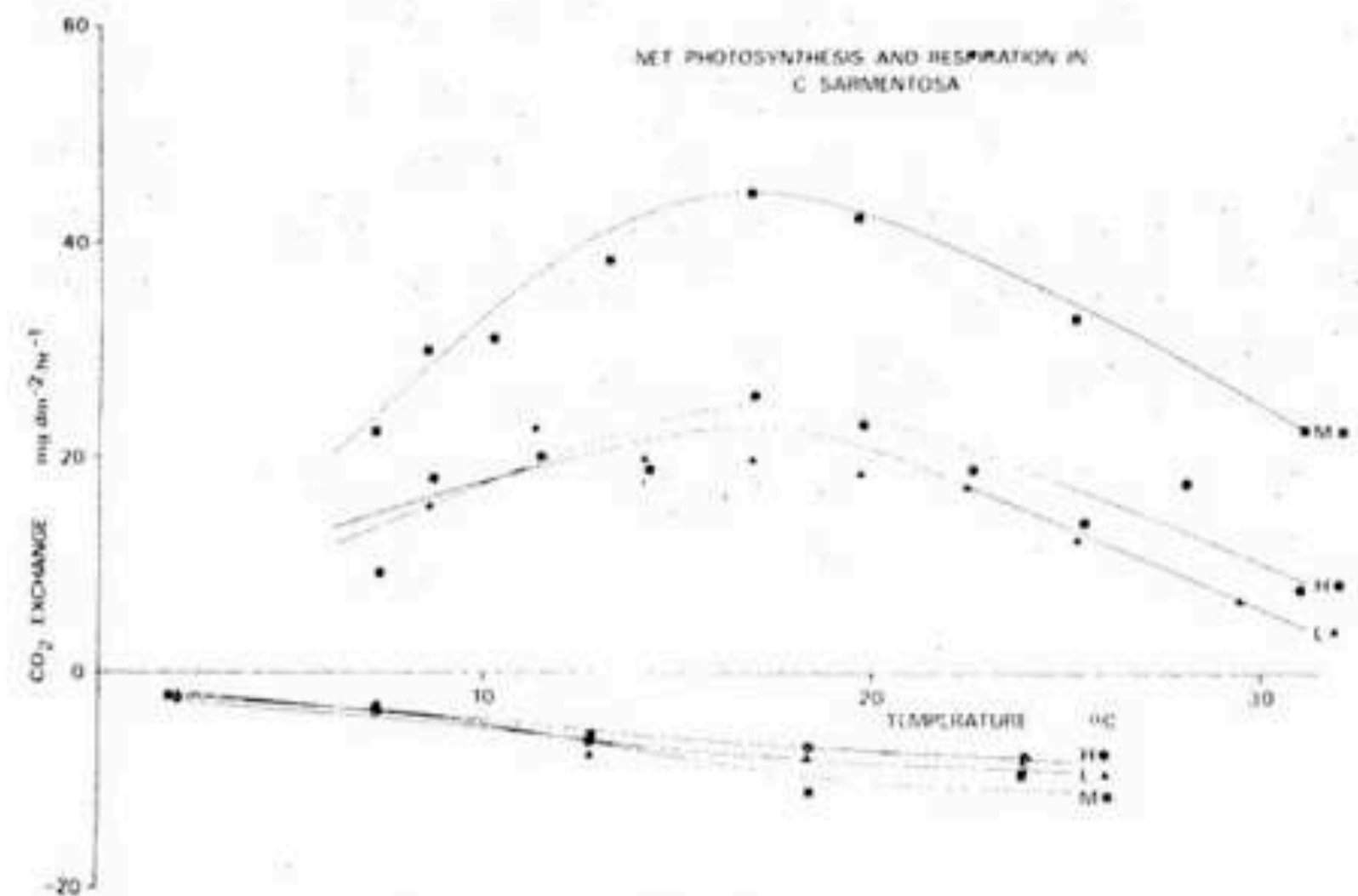


FIGURE 5. Net photosynthesis and dark respiration for *C. sarmentosa* at different leaf exposure temperatures. Curves represent trends for plants from different pre-treatment temperatures: H = High; M = Medium; L = Low.

The optimum temperature for photosynthesis appears to agree well both with optimum temperature for total plant growth and summer average temperatures for field sites.

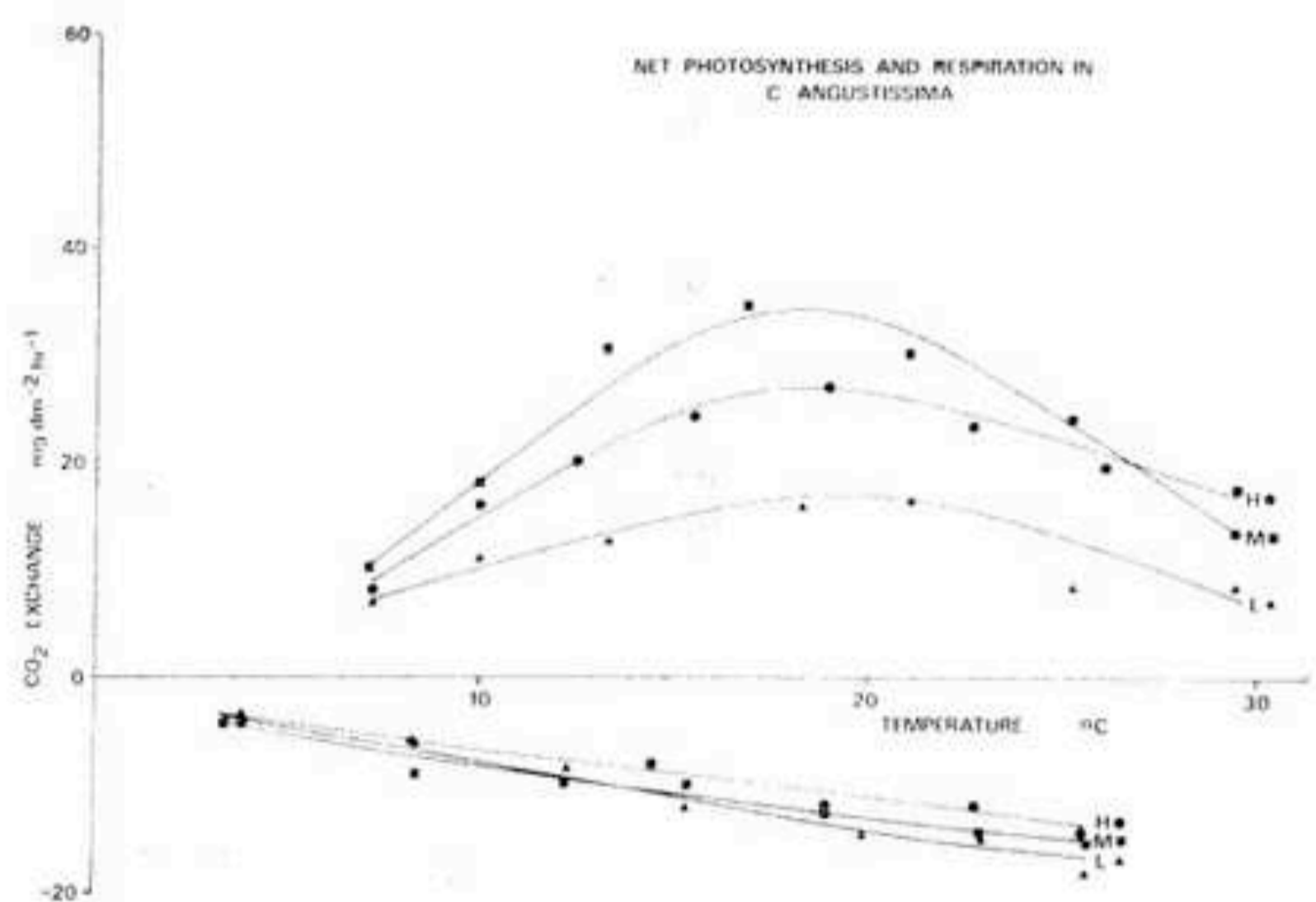


FIGURE 6. Net photosynthesis and dark respiration for *C. angustissima* at different leaf exposure temperatures. Curves represent average figures for plants from different pre-treatment temperatures: H = High; M = Medium; L = Low.

(ii) *Coriaria angustissima*

Changes in net PHS with temperature for this species, given in Figure 6, appear similar to those for *C. sarmentosa*. However, though the optimum temperature for net PHS of about 17°C is similar to that for the larger species, the maximum values of carbon dioxide assimilated appear somewhat lower. This is in accord with the relatively higher respiration values at all temperatures shown by the sub-alpine species.

b. *Acclimatisation to Previous Growing Temperatures*

Throughout the range of exposure temperatures the carbon dioxide exchange of *Coriaria* plants was markedly influenced by the previous growing temperature. This effect of pre-treatment temperature is demonstrated in Figure 5 for *C. sarmentosa*. Over the whole range of leaf exposure temperatures (5-30°C) plants pre-treated at 18°C (MT) had a net PHS greater than those from both 10°C (LT) and 24°C (HT) which were similar except at high temperatures. For *C. angustissima* (Figure 6) net PHS was again highest for the 18°C pre-treatment over most of the range. Low temperature pre-treatment for four months clearly had a depressing effect on short-term rate of carbon dioxide assimilation. Work on other species by Scott (1970), Rook (1969), McCree and Troughton (1969) and others has shown similar responses to pretreatment conditions.

Differences between respiration rates for both species also tended to vary according to pre-treatment temperatures. In both species, plants pre-treated at the high temperature had lowest respiration activity over all exposure temperatures. However, highest respiration rates were measured in plants grown at low temperatures in the case of *C. angustissima* and medium temperatures in *C. sarmentosa*.

c. *Change in Net Photosynthesis with Light Intensity*

In a different series of plants from the medium temperature growth cabinet, carbon dioxide exchange was determined for both species at illumination values from 20 K.lux down to darkness.

Temperature of the exposure chambers was set to 18°C (MT) and for dark respiration reduced to 10°C. Smoothed curves for the net PHS response to light in both species is shown as Figure 7. The difference between these two species in net photosynthesis—*C. sarmentosa* has higher rates over all light intensities—is consistent with results of the earlier comparisons at different exposure temperatures.

CHANGE IN NET PHOTOSYNTHESIS WITH LIGHT INTENSITY

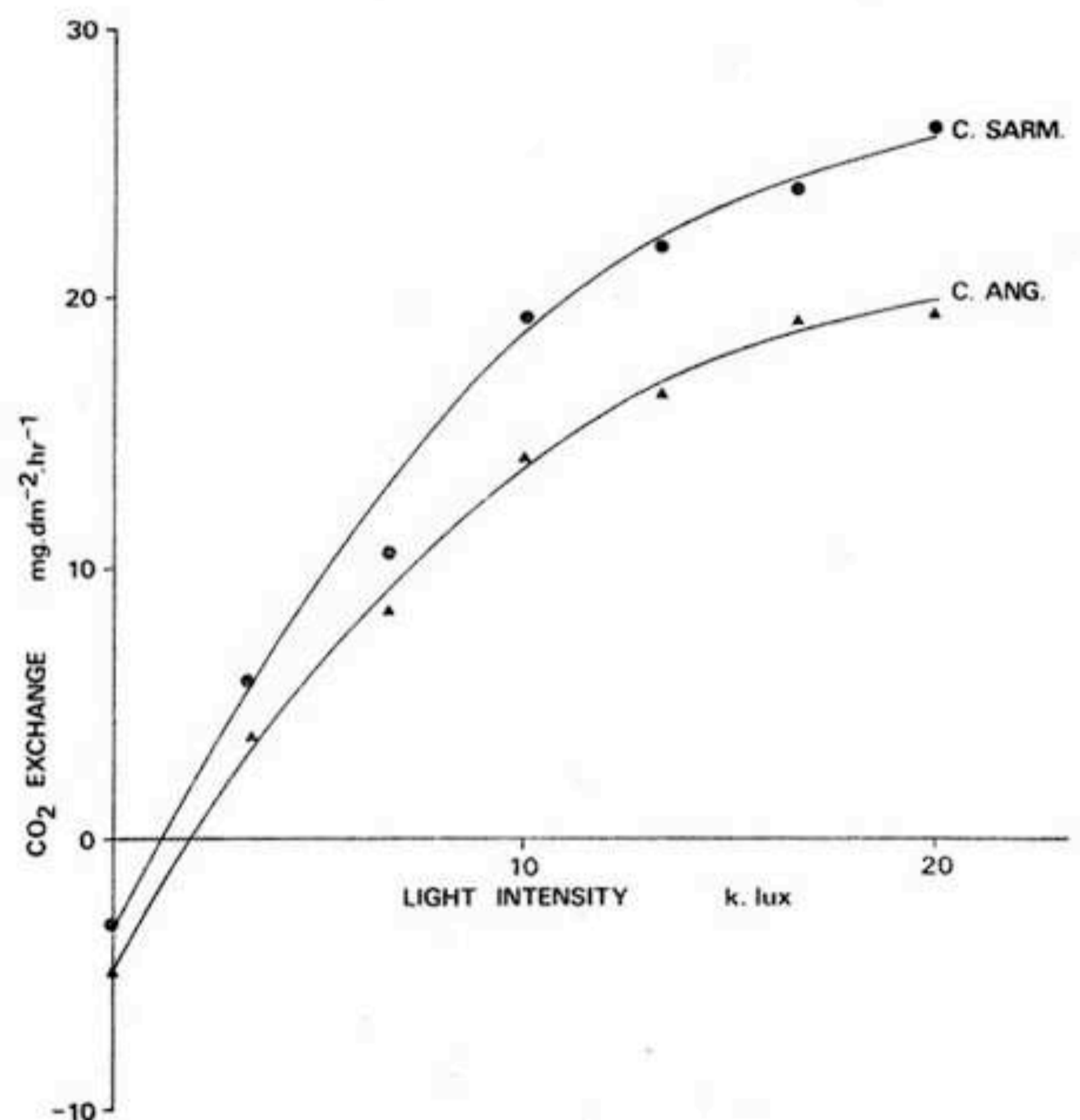


FIGURE 7. Response in net photosynthesis by *C. sarmentosa* and *C. angustissima* to change in light intensity at 22°C. Dark respiration was measured at 10°C.

The carbon dioxide exchange curves approach but do not reach equilibrium values at 2 K.lux intensity. Consequently it would be reasonable to assume a light level approaching those in full sunny conditions as the saturation level for tutu communities. This would be in keeping with the pioneer or successional ecological positions of these species. At the same time their high light requirement for growth is indicated by intolerance of shading and a high compensation point at approximately 2 K.lux.

## NITROGEN FIXATION BY ROOT NODULES

*Methods and Materials*

In order to follow up the response in nitrogen fixation shown by tutu with sulphur and phosphorus addition, the root nodules of all plants were excised and tested for nitrogenase activity. The method used throughout nitrogen fixation measurements both in the laboratory and the field has been that of acetylene reduction (Stewart *et al.* 1967).

*a. The Acetylene Reduction Method used for Assessing Nitrogenase Activity of Coriaria Root Nodules*

After washing plant roots their nodules were excised using forceps. Large coralloid clusters were then broken up to ensure even exposure to gas mixture. The excised nodules were again thoroughly washed in distilled water and distributed evenly into assay chambers. Each assay chamber used in this work was a 20ml disposable plastic syringe fitted with a 10cm rubber tube. To the other end of this tube a 22 gauge hypodermic needle was fitted. A mohr clip was used to hold or release gas through the needle.

Premixed gas phase (argon 70 per cent: oxygen 30 per cent by volume) was stored in a glass container with rubber tubing outlet. By manipulating the syringe, premixed gas phase could be drawn into the assay chamber and flushed out as required. After flushing, the assay chamber was filled with gas mixture to the 20ml mark. The actual capacity of the chamber when loaded was determined after each experiment.

A 2ml syringe was used to withdraw that volume of gas mixture from the assay chamber and replace it with acetylene. The chamber now containing 10 per cent  $C_2H_2$  was then incubated at a measured temperature for a specific time, usually 60min. For convenience, and as an extra precaution against leaks, the syringe needle tips were plunged into a rubber bung.

Ethylene production was detected by gas chromatography using a "Perkin-Elmer" F11 model fitted with a 4ft stainless steel column of "Poropak

T". Nitrogen flowing at 25-30ml/min. was the carrier gas and the detector was a hydrogen flame ionizer. For each chromatographic analysis 0.5ml of gas was extracted from the assay chamber by syringe and injected into the analyser. Triplicate samples were usually taken from each chamber. Ethylene production in micro moles can be calculated from a standard curve of peak heights for acetylene and ethylene.

Weight of dry matter in the exposed nodules was obtained after drying for 24 hours at 80°C. Values of acetylene reduction were expressed as micro moles acetylene reduced to ethylene per gram nodule dry matter per hour.

*b. Modifications for Use in the Field*

To avoid the use of glass apparatus two rubber bladders were used to carry gas mixtures required. Prepared immediately before a field trip, one bladder contained two litres of the argon:oxygen mixture, the other one litre of this mixture containing 10 per cent acetylene. Gas mixture was withdrawn through a cap by syringe. Incubated samples of nodules were killed by injecting 2ml of 50 per cent trichloro-acetic acid through the rubber tubing of each assay syringe. Assay syringes were returned to the laboratory for gas chromatographic analysis within two days of field exposure.

*Results and Discussion**a. Nitrogen Fixation in C. sarmentosa Root Nodules in Relation to Temperature*

The first nodules to be used in this work were excised from rhizome-cutting plants grown in potted field soil in the glasshouse.

The nitrogenase activity in excised nodules at different temperatures was measured in terms of acetylene reduction. A graph of results presented as Figure 8 indicates that optimum temperature for nitrogen fixation in grassland tutu may be between 20°C and 22°C. Because the plants used were grown in unfertilised, native soils, and exposures to acetylene were done in Spring, the rates of ethylene production may be somewhat lower than possible.

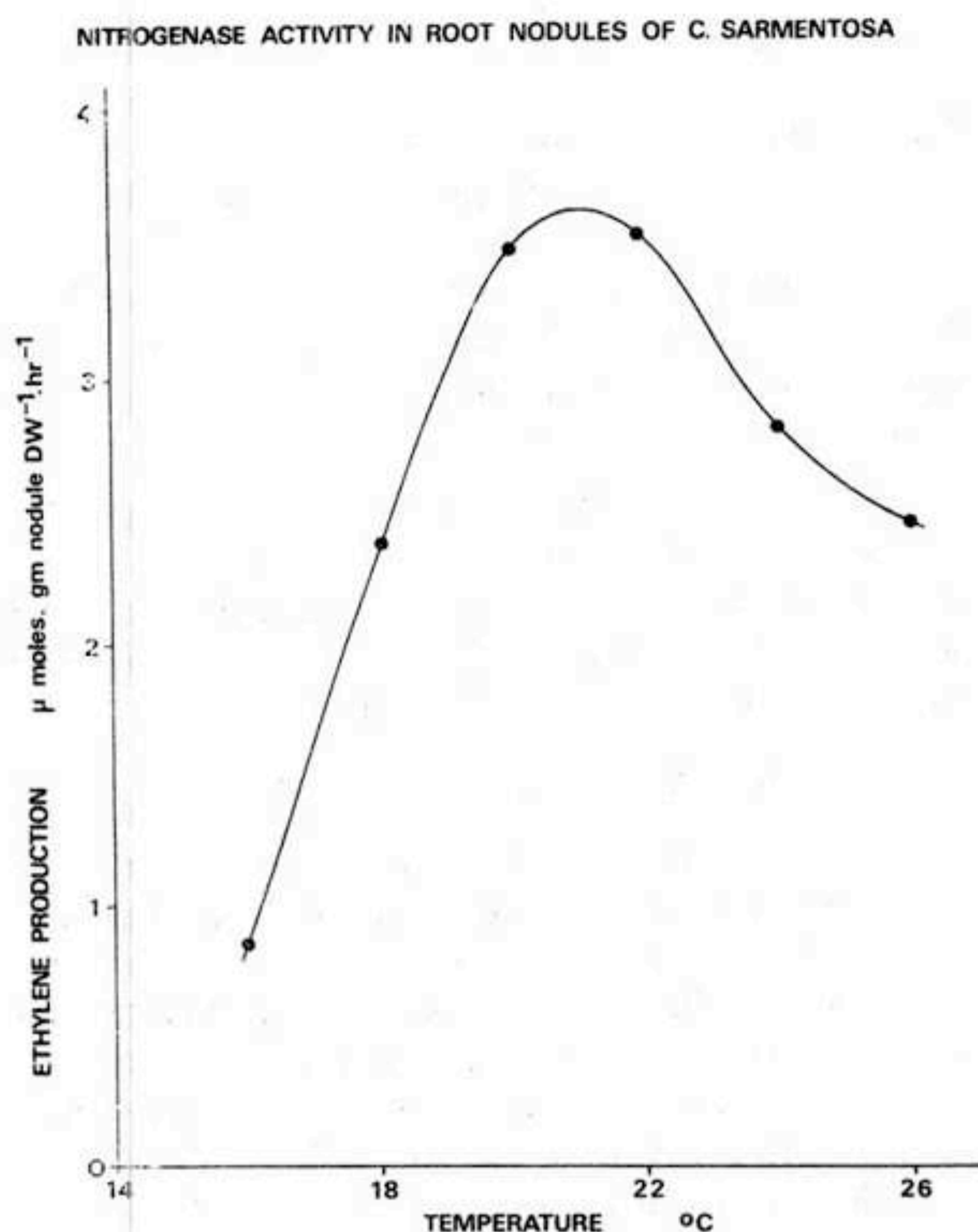


FIGURE 8. Effect of temperature on nitrogenase activity in excised root nodules of *C. sarmentosa*.

b. *Nitrogenase Activity in Rhizomatous Species of Coriaria in Relation to Previous Temperatures*

The root nodules of all 144 plants in the factorial growth chamber, species, soil and fertiliser experiment were tested at harvest in July for nitrogenase activity. All nodule samples were found to be active to a greater or lesser degree. Table 3 sets out average nodule activity at 22°C as micro moles ethylene produced per gram dry matter per hour ( $\mu\text{mole/gD.W./h}$ ) for each of the four clones of *C. sarmentosa* from the three pre-treatment temperatures. There are considerable differences in activity between clones and between nodules from the three different growing temperatures. Nodules of the clone from Goldney Saddle seem consistently higher in ethylene production than do those of the other three.

TABLE 3. Rate of Nitrogen Fixation in Excised Root Nodules of *C. sarmentosa* at 22°C.

(Acetylene Reduced in  $\mu$  mole/gm nodule D.W./Hour)

Clone	Pretreatment Temperature °C		
	10/3	18/10	24/16
Hunua	0.54	0.77	0.60
Craigieburn R.	0.11	0.21	0.86
Goldney Saddle	0.70	1.17	3.88
Arthurs Pass	0.64	0.24	1.32
Average Value	0.50	0.56	1.65

Again, the nitrogenase activity of nodules rose from plants pre-treated with low temperatures to those previously experiencing high temperatures. Table 4 shows that the effect of pre-treatment temperature on rate of ethylene production is reversed for excised nodules of *C. angustissima*. As before one clone is markedly superior to the other three in acetylene reduction by root nodule samples. However, nodule efficiency in nitrogen fixation appears to be of the same order for both species. These results are comparable to many obtained with the same method for other nodulated non-legumes, legumes and concentrated blue-green algae blooms (Stewart *et al.* 1967, Silver 1969, Sloger 1968).

TABLE 4. Rate of Nitrogen Fixation in Excised Root Nodules of *C. angustissima* at 22°C.

(Acetylene Reduced in  $\mu$  mole/gm nodule D.W./Hour)

Clone	Pretreatment Temperature °C		
	10/3	18/10	24/16
1	0.95	0.07	0.15
2	1.27	0.27	0.04
3	2.07	3.02	2.44
4	1.00	0.20	1.60
Average Value	1.32	0.89	1.05

c. *Nitrogenase Activity of C. sarmentosa in the Field*

Field exposures of young and old nodules, soil around the plants and grassland tutu root systems yielded the interesting results summarised in



TABLE 5. *Root Nodule Activity of C. sarmentosa in the Field.*(Acetylene Reduced  $\mu$  moles/gm nodule D.W./Hour)

Field Site	Season	Young Nodules	Old Nodules	Root System	Soil
Hunua	Spring	1.22	0.48	Trace	0.02
Goldney Saddle	Spring	0.82	0.01	Trace	Trace
Arthurs Pass	Late Summer	72.5	16.2	1.07 { +small [ nodules ]	0.01

Table 5. The clonal site difference appears less important than the seasonal effect on rate of nitrogen fixation. The extremely high rate of ethylene production by nodules at Arthur's Pass needs to be confirmed. However, Sloger (1968) did achieve rates of the order of  $20\mu$  moles/g D.W./h in the nodules of *Myrica cerifera* in Florida.

The loss of nodule efficiency with nodule maturity is also clearly seen in these results. Increase in non-active tissue and cork as a proportion of total nodule dry matter doubtless has much to do with this ontogenetic drift in rate of nitrogen fixation.

#### GENERAL DISCUSSION

Do these results confirm or change any of our ecological assumptions concerning rhizomatous tutu in its field behaviour?

For many years *C. sarmentosa* was considered to lack nodules. In the mature patches of tutu searched by Morrison and Harris (1959) it is very likely that nodule function had deteriorated from both age and adequacy of other sources of combined nitrogen. Consequently many nodule clusters would have died and been lost from the roots.

Field observations show now that nodulation is vigorous only on young plants and those forming new rhizomes in successional soils. As the soil pH, aeration, sulphur and phosphorus level are reduced and soil organic matter increased, nodulation and nodule formation would be impaired; but, in addition, though tutu nodules are perennial, their efficiency is gradually reduced

with age. This is clearly demonstrated by the rate of acetylene reduction, which is high in young nodules and very low in old tissue.

The information on plant growth, net carbon fixation and nitrogen fixation is consistent with the successional position of these tutu species in the field. They have high requirements for light energy and available sulphur and phosphorus. Active nitrogen fixation is dependent upon an abundant oxygen supply to root nodules. The shoots are very intolerant of even the slightest water stress and frost damage. Thus the species are restricted to montane valleys and wet, well-aerated successional sites and young soils.

Their use in the revegetation of moist screes up to timberline has not yet been fully tested. Certainly the high unseasonal frost damage experienced by plants transplanted to 1700m in the Craigieburn Range rules out their use in alpine revegetation work. Below 1300m growth of transplants may be vigorous, especially from cuttings raised after applying superphosphate. However, natural establishment, where it does occur, is so successful that we are encouraged to more detailed autecological study of rhizomatous tutu species. The formation of rhizomes is extremely vigorous in both species and their ability to bind rock and gravel on steep slopes is demonstrated effectively in natural habitats.

Questions to be answered include, how can dormancy be broken in large numbers of seeds in order to improve germination and seedling establishment? Are there advantages to be gained in selecting clonal lines from ecologically adapted populations? There are relatively few native species showing promise in attempts to revegetate

the eroded greywacke mountains. Rhizomatous *Coriaria* may yet prove to be valuable in the repair of specialised sites.

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