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SOIL-PLANT RELATIONSHIPS IN A *EUCALYPTUS* FOREST ON THE SOUTH COAST OF NEW SOUTH WALES

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Abstract. The chemical and physical soil characteristics of the *Eucalyptus* associations in Benandra State Forest are described. Changes in species associations occur over a gradient of increasing moisture and nutrient status of soils from ridge to gully sites. Concentrations of major nutrients in leaves and bark of dominant trees on these sites generally follow the soil gradients. In particular, leaf phosphorus and bark calcium are correlated with the corresponding soil nutrients. Soil calcium and magnesium are also correlated with leaf phosphorus, indicating a possible interaction between these soil nutrients and phosphorus uptake by the trees. Soil magnesium is similarly correlated with bark calcium. Aluminum is the major exchangeable cation in soils of the poorer ridge sites which are the most acid. It is hypothesized that soil aluminum competes with other nutrient cations such as calcium and magnesium for sites of absorption on plant roots. In addition to the effect of soil pH on phosphate solubility, competition between aluminum ions and other cations may inhibit the absorption and uptake of calcium and phosphorus, both of which are important to the growth and nutrition of the *Eucalyptus* species in the study area.

Eucalyptus forests of southeastern Australia can be described as a changing mosaic of species associations with gradual changes in the composition of species along gradients of soil nutrients and soil moisture regimes (Florence 1963, 1964). In addition to the species distributions along edaphic gradients, *Eucalyptus* species also exhibit sensitive interspecific relationships which vary with minor habitat variations (Pryor 1959). The influence of certain species on their own sites may also contribute to their sensitivity to minor habitat variations (Florence and Crocker 1962, Florence 1964).

The main purpose of this present investigation is to describe some of the soil-plant relationships of the natural *Eucalyptus* associations in an area that is typical of many areas of *Eucalyptus* on the east coast of Australia, where species associations appear to be related to a general gradient of edaphic characteristics. This study is complementary to the study of McColl and Humphreys (1967) which was conducted in the same area. They showed that the separation of the closely related species, *E. gummifera* (Gaertn.) Hochr. and *E. maculata* Hook. into discrete stands with often contiguous boundaries is not clearly associated with any marked edaphic discontinuity, but occurs across a general gradient in soil properties. This was in contrast to statistically significant differences found between species in nutrient concentrations of leaves and bark. In this present report the general gradient of soil properties is described, and interpretations of some of the soil-plant relationships are made from results of soil

and plant tissue analyses, soil moisture determinations and a glasshouse pot trial.

DESCRIPTION OF THE STUDY AREA

Study sites were selected in Benandra State Forest, which covers about 2,800 ha, near Batemans Bay on the south coast of New South Wales, Australia.

The mean annual rainfall is about 1,000 mm, and the mean monthly rainfall is about 65 mm in winter and 135 mm in summer. Mean monthly temperatures are 10.5°C in winter, and 20.0°C in summer. Ordovician metamorphosed sediments comprise the main geological formations. The topography varies between 30–120 m above sea-level. McColl and Humphreys (1967) have already described the area in terms of climate, geology and dominant vegetation, but for convenience the description of the vegetation is given here also.

The dominant vegetation can be suitably characterized by four *Eucalyptus* "associations":

1) The *E. gummifera* dry sclerophyll association occurs on ridges on relatively shallow red to yellow podzolic soils. Species often codominant with *E. gummifera* include: *Angophora intermedia* D.C., *Casuarina* sp., *Eucalyptus globoidea* Blakely, *E. pilularis* Sm., *E. piperita* Sm., *E. sieberiana* F. Muell.

2) The *E. maculata*-*E. paniculata* Sm. dry sclerophyll association occurs on moderate slopes on brown to yellow podzolic soils. Codominant species include: *Eucalyptus globoidea*, *E. muellerana* Howitt., *E. pilularis*, *E. piperita*, *E. sieberiana*.

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3) The *E. maculata*-*E. pilularis* dry sclerophyll association occurs on slopes in a discontinuous manner with the *E. maculata*-*E. paniculata* association. The discontinuous distributions of the two associations on the slopes is primarily related to changes in soil parent materials. The *E. maculata*-*E. paniculata* association generally occurs on soil derived from shale or micaceous sandstone, whereas the *E. maculata*-*E. pilularis* association usually occurs on soil from slate or schist parent material.

4) The *E. saligna* Sm. wet sclerophyll association occurs in the gullies on kraznosem (i.e. lato-sol) soils. In some locations, *Eucalyptus botryoides* Sm. is codominant and forms hybrid swarms with *E. saligna*. Rainforest species are often present and the understory species are usually more mesomorphic than those of the other sites.

Narrow ecotones exist between the *E. maculata*-*E. paniculata*, *E. maculata*-*E. pilularis*, and *E. gummiifera* associations, and also between the *E. maculata*-*E. paniculata*, *E. maculata*-*E. pilularis* and *E. saligna* associations.

METHODS

Four sites were chosen in Benandra State Forest as representative of the four main associations, after extensive field observations were made. Each site was 0.04 ha. The designation of these sites, by associations, is the same as that just described.

Soil sampling and analysis

Soil used in the pot trial was taken from the 0-15 cm depth at four-six places at each site. Soil for each site was thoroughly mixed, then passed through a 2.5-cm sieve. Samples for physical and chemical analyses were taken from three places at each site at 8-12 cm and 48-52 cm depths. About 100 g were then taken from each sample, air-dried, then passed through a 2-mm sieve. Stone content at the 8-12 cm depth was determined as the fraction by weight over 2 mm diameter.

Bulk density samples were taken from the surface soils at six places at each site. Bulk densities for soil lower in the profiles were estimated from the regression equation, $y = 0.83 + 0.01x$, where y = bulk density (grams per cubic centimeter), and x = sand (percentage); for this equation, $df = 13$, $r = 0.73$ (significant at the 0.01 level). This equation was computed from data collected in the study area which are presented both in this report and that of McColl and Humphreys (1967).

Soil textural analyses were made in duplicate using the hydrometer method (Bouyoucos 1936, 1953), and the International System for textural classification. Field capacity (FC) determinations

TABLE 1. "Rooting depths" and moisture characteristics in "rooting zone" of soils at sites supporting the four *Eucalyptus* associations in Benandra State Forest, New South Wales

Characteristic	Association			
	<i>E. gummiifera</i>	<i>E. maculata</i> - <i>E. paniculata</i>	<i>E. maculata</i> - <i>E. pilularis</i>	<i>E. saligna</i>
"Rooting depth" (cm)	92	122	102	122
Field capacity (mm of water)	182	422	371	410
Permanent wilting point (mm of water)	125	200	173	276
*Mean soil moisture over study period (mm of water)	165	244	243	378

*Least difference for significance between means at the 0.05 level = 87.

were made using the pressure plate apparatus at 0.1 atm, and permanent wilting point (PWP) determinations were made using the pressure membrane apparatus at 15 atm, on the sieved-soil samples (Slatyer and McIlroy 1961).

Soil moisture determinations were made in triplicate at each site, every 6 weeks throughout a 14-month period. Samples were taken with an auger at 8-12 cm, 48-52 cm and 98-102 cm depths. Moisture contents were determined gravimetrically and means calculated as percentages of the oven-dry weights of the sieved soil. Effective "rooting depths" (Table 1) were estimated from field observations of the soil profiles. The samples from the three depths were taken as typical of particular horizons of each soil. The total quantity of soil water in the "rooting zone" was calculated from the percentage moisture content, taking bulk density into account.

Total phosphorus, pH, and the exchangeable cations, aluminum, calcium, magnesium, potassium and sodium, were also determined, using the methods previously described by Gentle, Humphreys, and Lambert (1965) and McColl and Humphreys (1967). Nutrient concentrations at the 8-12 cm and 48-52 cm depths were taken as representative of the 0-15 cm and the 15-61 cm depths, respectively. The total quantity (kg/ha) of each nutrient in the 0-61 cm depth was calculated for each site, taking bulk density into account.

Plant tissue sampling and analysis

Tissue sampling was carried out in July 1964. Leaf samples (about 60g/tree) of the previous year's growth were taken from the upper crowns of six dominant trees of a species at each site. Four bark samples were taken from three dominant trees of each species at each site, at positions facing the cardinal points, 50-100 cm above ground level. Subsamples were mixed together for each

species at each site, for leaves and bark respectively. Concentrations of phosphorus, aluminum, calcium, magnesium, potassium, sodium, manganese and zinc in the tissues were determined using the methods described by Gentle, Humphreys and Lambert (1965) and McColl and Humphreys (1967).

Pot trial

Soil was sampled from each site representing the four associations, as described earlier; 500 g were placed in each 10 cm diameter plastic pot in a glasshouse. *Eucalyptus gummifera*, *E. piperita*, *E. pilularis*, *E. paniculata*, *E. maculata* and *E. saligna* were raised from seed collected by the author in the study area. All species were grown in soil from all sites. There was one seedling per pot, and four replicates of each soil-species combination were set up in a randomized design. Randomization was done each week. *Eucalyptus piperita*, *E. pilularis* and *E. saligna* were harvested after 13 weeks, *E. maculata* after 20 weeks, and *E. paniculata* after 30 weeks. The difference between harvest times was due to demand for limited glasshouse space. Leaf numbers, leaf areas, shoot heights, and dry weights of roots and shoots were measured at harvesting.

Statistical analysis

Standard errors of means (SE), analyses of variance, and least differences for significance between treatment means (LSD) at the 0.05 level, using Tukey's *Q* test, were computed following the methods of Snedecor (1956). Simple linear correlation coefficients (*r*) were also computed (Snedecor 1956), to help characterize the relationships between nutrient levels in soil and plant tissues. Data used in the computation of these coefficients include those given in the results of this paper as well as those used by McColl and Humphreys (1967).

RESULTS AND DISCUSSION

A general gradient in most soil properties exists from the site supporting the *E. gummifera* association, through those of the discontinuous *E. maculata*-*E. paniculata* and *E. maculata*-*E. pilularis* associations, to that of the *E. saligna* association. The change in soil properties is largely an effect of the change in topography, although differences in parent materials also have some effect.

Soil moisture regime

The gradient is shown by the periodic total quantities of soil water in the "rooting zone" over a 14-month period (Fig. 1). Mean values for the

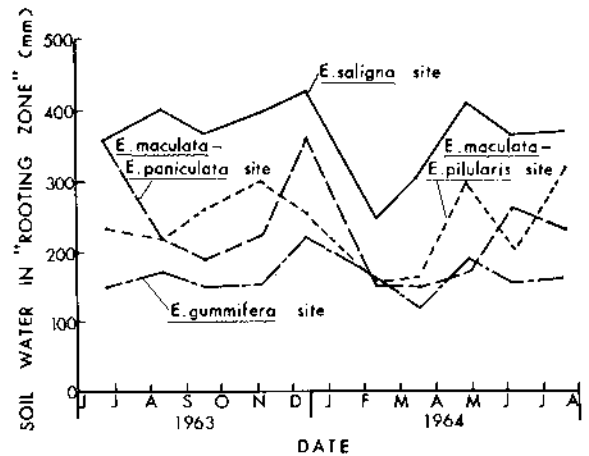


FIG. 1. Total soil water in "rooting zone" at sites supporting the four *Eucalyptus* associations in Benandra State Forest, New South Wales.

four sites are given in Table 1. The values for species associations of the slopes (sites 2 and 3) fall between the *E. gummifera* ridge site (site 1) which is the driest, and the *E. saligna* gully site (site 4) which is the wettest. A reasonable estimate of available moisture is often given by the quantity of water that exists in a soil between FC and PWP, but caution is advised in the use and interpretation of these parameters as they vary between soils and between plant species (Slatyer 1967). Values of FC and PWP are given (Table 1) for comparative purposes only, and are not meant to represent definite limits of available soil moisture. At all sites, the soil moisture values did drop below PWP, and in some instances did rise above FC (Fig. 1, Table 1). The species studied are resistant to wilting at the 15 atm tension represented by PWP. The techniques of PWP and FC determinations are also open to criticism. The soil of the *E. saligna* association (Table 1) was never observed to be waterlogged in the field, although moisture contents were above the laboratory determined FC on a couple of occasions.

Soil nutrient regime

Results of the physical and chemical analyses also illustrate the gradient in soil properties from ridge to gully (Table 2). On the ridges, particularly where the surface soil has a high sand content, well-leached podzolic soils develop. These soils, supporting the *E. gummifera* association, are commonly derived from quartzite and shale parent materials. As a consequence of the high soil moisture flow rates in these sandy soils, and also because of the lower potential nutrient supply afforded by the quartzite parent material, the level of exchangeable mineral nutrient cations (except-

TABLE 2. Chemical^a and physical characteristics of soils at sites supporting the four *Eucalyptus* associations in Benandra State Forest, New South Wales. (Means \pm SE, where $n = 3$)

Characteristic	Associations			
	<i>E. gummifera</i>	<i>E. maculata- E. paniculata</i>	<i>E. maculata- E. pilularis</i>	<i>E. saligna</i>
8-12 cm depth				
Total P (ppm)	170 \pm 94	293 \pm 20	98 \pm 26	469 \pm 54
Exchangeable cations (meq/100g)				
Al	1.91 \pm 0.15	1.46 \pm 0.64	0.70 \pm 0.35	0.15 \pm 0.08
Ca	0.81 \pm 0.43	3.82 \pm 1.92	3.04 \pm 0.91	4.46 \pm 1.39
Mg	0.72 \pm 0.30	3.28 \pm 0.52	1.47 \pm 0.43	5.76 \pm 1.11
K	0.09 \pm 0.02	0.47 \pm 0.06	0.19 \pm 0.07	0.45 \pm 0.06
Na	0.06 \pm 0.02	0.17 \pm 0.02	0.09 \pm 0.03	0.24 \pm 0.05
pH (1:1, soil:water)	4.45 \pm 0.04	5.30 \pm 0.13	5.54 \pm 0.23	5.82 \pm 0.04
Sand %	73.0	46.7	43.6	43.3
Silt %	15.6	25.0	34.4	25.0
Clay %	11.4	28.3	22.0	31.7
Stone %	46.5	50.8	22.6	3.2
Bulk density (g/cc)	1.36	1.09	1.08	1.18
48-52 cm depth				
Total P (ppm)	328 \pm 42	245 \pm 67	89 \pm 15	262 \pm 16
Exchangeable cations (meq/100g)				
Al	7.64 \pm 1.39	5.19 \pm 1.65	2.51 \pm 0.79	0.77 \pm 0.56
Ca	0.11 \pm 0.03	0.19 \pm 0.05	0.39 \pm 0.16	2.97 \pm 1.70
Mg	0.79 \pm 0.16	3.56 \pm 1.18	0.79 \pm 0.17	3.81 \pm 1.15
K	0.15 \pm 0.02	0.15 \pm 0.05	0.11 \pm 0.11	0.40 \pm 0.14
Na	0.05 \pm 0.01	0.23 \pm 0.10	0.03 \pm 0.01	0.26 \pm 0.03
pH (1:1, soil:water)	4.97 \pm 0.13	5.51 \pm 0.02	5.25 \pm 0.09	5.84 \pm 0.09
Sand %	49.7	48.3	37.4	43.3
Silt %	12.1	21.7	29.0	15.0
Clay %	38.2	30.0	34.6	41.6
Bulk density (g/cc)	1.33	1.31	1.20	1.26
Total amount (kg/ha) in the 0-61 cm depth				
Total P	2,349 \pm 321	1,954 \pm 405	650 \pm 94	2,350 \pm 134
Exchangeable cations				
Al	4,538 \pm 760	3,016 \pm 898	1,348 \pm 396	420 \pm 291
Ca	470 \pm 180	1,491 \pm 814	1,428 \pm 345	5,032 \pm 2,023
Mg	765 \pm 140	3,255 \pm 868	821 \pm 142	3,925 \pm 842
K	430 \pm 51	655 \pm 123	358 \pm 50	1,217 \pm 319
Na	94 \pm 24	382 \pm 147	72 \pm 17	443 \pm 44

^aChemical analyses by F. R. Humphreys.

ing aluminum) is very low (Table 2). The concentration of exchangeable aluminum at site 1 is much higher, both at the 11 and 51 cm depths, than at the other sites. *Eucalyptus gummifera* soils also have a greater accumulation of hydrogen ions which replaced leached bases. This greater acidity (Table 2) brings about the increase in solubility of aluminum which is carried down in the profile and deposited in the B horizon. (Compare aluminum contents at the 8-12 cm and 48-52 cm depths at site 1, Table 2).

Soil moisture flow rates would be slower on the slopes (sites 2 and 3) where the surface soils have a higher clay content (Table 2). Soil moisture is also enriched in soluble products transported from

higher ground. Thus, less-leached, less acidic, deeper, podzolic soils occur which are generally higher in mineral nutrient content than those of the ridges (Table 2). Soils of both the *E. maculata-E. paniculata* and *E. maculata-E. pilularis* associations have lower bulk densities than those supporting the *E. gummifera* association, but stone contents at the 8-12 cm depth are variable (Table 2).

In the gully sites, which support the *E. saligna* association, eroded soil and products of weathering accumulate, and soil leaching is less severe. Mildly acid, often deep, kraznosem (i.e. latosol) soils develop from alluvial parent material which is also enriched in nutrients transported from higher

ground. The nutrient supply of these soils is high, particularly as the stone content is very low (Table 2). The low stone content allows a large volume of soil to be easily exploited by roots. The sheltered gully sites also support some rainforest species. Infrequency of fires plays an important role in the maintenance of this mesomorphic vegetation. Fires are more frequent in the forest associations on the slopes and ridges, according to the author's field observations and unpublished reports of local forestry officers.

Results of the pot trial also indicate the gradient in soil nutrient levels from ridge to gully sites (Fig. 2). Leaf numbers, leaf areas and shoot heights were closely correlated with shoot dry weights, so results are expressed as shoot dry weights only. Specificity of the species for their natural soil was not apparent. *Eucalyptus gummifera*, *E. pilularis*, and *E. piperita*, which are species occurring on the poorer sites in the field, were, however, more tolerant of the lower nutrient soils than were *E. paniculata*, *E. maculata*, and *E. saligna* which usually occur on the better sites.

Reduced growth of the species in soils of sites 1 and 2 especially, is due to nitrogen, phosphorus, and calcium deficiencies (McCull and Humphreys 1967). Lower shoot:root ratios (Fig. 2) also indicate these deficiencies (Pirson 1956).

The relative proportions of soil calcium and magnesium at sites 1 and 2 are much less favorable for plant growth than those at sites 3 and 4 (Table 2). Much work has been done relating the status of soil calcium and magnesium to plant distribution and growth (e.g. Walker 1954). Where the calcium:magnesium ratio is less than 1, magnesium may compete with calcium to the extent of limiting growth, owing to insufficient soil calcium being available for absorption. There is little evidence indicating the importance to growth of such an interaction from data of this present study. The interaction of exchangeable calcium and magnesium with exchangeable aluminum, however, is discussed later.

Plant tissue nutrient regime

The gradient in soil nutrient cation levels, except sodium and aluminum, is reflected in the levels of nutrients in leaves and bark of dominant trees of the species naturally occurring at the four sites (Table 3). Sodium concentrations are quite variable between species (Table 3). The study area is located on the coast where winds carry salt spray inland from the ocean. The concentration of this salt in rainwater is dependent on distance from the coast (Hutton 1958), as well as other factors such as local topography. Sodium concentrations in the soil and plant tissues may, therefore, be more dependent on atmospheric sources rather than the soil parent material. Humphreys (unpublished) demonstrated this when he found a close correlation between sodium contents of *Pinus* foliage and distance from the coast of eastern Australia. In spite of the high aluminum concentrations in the soils (Table 2), particularly at site 1, the leaf and bark concentrations are quite low (Table 3). These species are not, therefore, aluminum accumulators, and generally contain much less foliar aluminum than do pines growing on the same or similar sites (Humphreys 1964a). Aluminum is not, itself, usually regarded as essential for tree growth (Kramer and Kozlowski 1960), but may play an important role in the uptake of phosphorus, as discussed later. Manganese and zinc concentration in leaves (Table 3) tend to be higher on sites with higher phosphorus concentrations in the surface soils. Similarly, on an acid, sandy soil, increasing levels of phosphate fertilization were associated with increasing zinc and manganese concentrations in citrus foliage (Reuther et al. 1949).

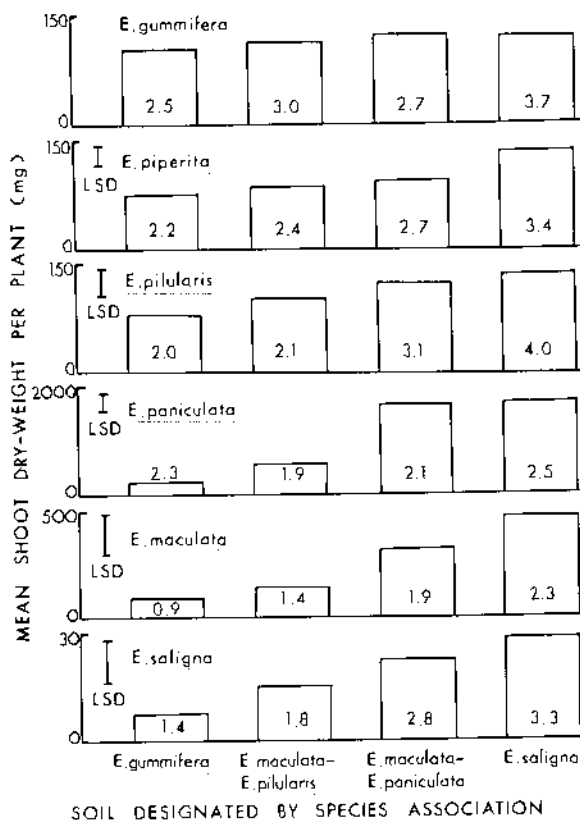


FIG. 2. Seedling growth of *Eucalyptus* species in surface soils from sites supporting the four *Eucalyptus* associations in Benandra State Forest, New South Wales. (Shoot:root dry-weight ratios are shown in bars. LSD = least difference between means for significance at the 0.05 level).

TABLE 3.^a Concentrations of nutrients in leaves and bark of dominant trees of *Eucalyptus* species at sites supporting: 1, *Eucalyptus gummifera*, 2, *E. maculata*-*E. paniculata*, 3, *E. maculata*-*E. pilularis*, and 4, *E. saligna* associations in Benandra State Forest, New South Wales. (Means of bulked samples where $n = 3$ for bark, and $n = 6$ for leaves)

Nutrient (ppm)	Site number and species					
	1 <i>E. gummifera</i>	2 <i>E. maculata</i>	2 <i>E. paniculata</i>	3 <i>E. maculata</i>	3 <i>E. pilularis</i>	4 <i>E. saligna</i>
P leaves	341	727	793	524	597	756
bark	390	420	450	350	250	560
Al leaves	140	82	110	182	134	118
bark	190	50	40	100	120	nil
Ca leaves	3,364	5,815	8,516	7,534	2,998	3,957
bark	6,400	28,000	21,000	11,800	2,200	35,400
Mg leaves	1,769	2,494	3,078	2,240	3,311	3,522
bark	600	900	1,200	1,900	700	1,600
K leaves	5,223	9,451	4,619	9,398	3,717	5,924
bark	1,600	3,100	2,600	4,100	1,900	4,100
Na leaves	3,591	2,268	3,049	2,209	1,998	1,787
bark	1,000	500	1,300	900	800	2,700
Mn leaves	98	362	764	450	136	320
Zn leaves	14	41	13	35	16	20

^aChemical analyses by F. R. Humphreys.

TABLE 4. Correlations between concentrations of nutrients in surface soils with the concentration of the same nutrient in the leaves and bark of *Eucalyptus* species in Benandra State Forest, New South Wales. Simple correlation coefficients for the correlations of both leaf phosphorus and bark calcium with various soil nutrients, are given in the lower portion of the table. (Logarithmic transformations used throughout. $df = 14$ in all cases)

Nutrient	Correlation coefficients	
	Soil vs. leaves	Soil vs. bark
Phosphorus	0.609*	NS
Aluminum	NS	NS
Calcium	NS	0.538*
Magnesium	NS	NS
Potassium	NS	NS
Sodium	NS	NS

Tissue nutrient	Soil nutrient				
	P	Al	Ca	Mg	K
Leaf P	0.609*	NS	0.631*	0.706**	NS
Bark Ca	NS	NS	0.538*	0.539*	NS
	Na	P×Ca/ Al	Ca/Al	P/Al	
Leaf P	NS	0.651**	0.531*	0.548*	
Bark Ca	NS	—	—	—	

NS = not significant
 * = significant at the 0.05 level
 ** = significant at the 0.01 level

Soil-plant nutrient relationships

Analyses of relationships between plant nutrient levels and the levels of the corresponding soil nutrients for the genus as a whole revealed signifi-

cant correlations of leaf phosphorus with soil phosphorus, and bark calcium with soil calcium (Table 4). There are relatively few reports where such correlations have been observed between soil and tree tissue nutrient levels, although attempts have been made (e.g. McVickar 1949, Metz, Wells and Swindel 1966). The correlation between soil phosphorus and needle phosphorus of *Pinus elliottii* Engelm. in a plantation in New South Wales (Baur 1959) is one exception. Shomaker and Rudolph (1964) also related soil phosphorus with both leaf phosphorus and growth of *Liriodendron tulipifera* L., and similar results for other species were found by Bard (1945) and Walker (1956) with phosphorus. Phosphorus and calcium have previously been found to be important factors of nutrition of individual species in Benandra State Forest (McCull and Humphreys 1967), as well as being controlling factors of distributions of *Eucalyptus* species elsewhere. Beadle (1954, 1962), for example, indicated that plant communities of the central coast of New South Wales, which include *Eucalyptus* species, are delimited by the amount of available soil phosphorus. On the southern tablelands of New South Wales, Moore (1959, 1961) found that the distributional patterns of *E. melliodora* A. Cunn. and *E. rossii* Baker and Smith, appear to be controlled by interspecific competition for exchangeable soil calcium.

Other soil nutrients are also correlated with leaf phosphorus and bark calcium (Table 4). Soil calcium is significantly related to leaf phosphorus thus supporting the hypothesis that phosphorus uptake is closely related to the amount of calcium

available to the roots. Calcium has been noted to increase root elongation (Pirson 1956), to increase HPO_4^- absorption (Leggett 1956), and to increase phosphorus uptake (Tanada 1955). Soil magnesium is similarly correlated with leaf phosphorus and bark calcium (Table 4). This may be an indirect relationship, as calcium and magnesium in the soil are themselves closely correlated ($r = 0.862$, significant at the 0.001 level, from present data and that of McColl and Humphreys (1967)). The relationship between soil magnesium and leaf phosphorus may, however, reflect the importance of magnesium on phosphorus reactions in the plant. Magnesium has also been found to have a positive correlation with phosphorus uptake in apple trees (Mulder 1953).

Total soil phosphorus does not always give a reasonable measure of phosphorus available for absorption by plants. It is the soluble form that is nutritionally important. Phosphate solubility is largely determined by soil pH (Wiklander 1958). Over the pH range (4.5–6.0) of soils in this study, phosphate solubility markedly drops with a decrease in pH. Soil calcium exerts a strong influence on pH; with an increase in calcium there is also an increase in pH. Consequently, at a high pH, more phosphorus becomes available in a soluble form for absorption.

Interaction of cations at the root surface may also affect phosphorus absorption. The amount of a given cation absorbed on the exchange sites can be inhibited by another cation if present in excess, especially if it has a greater affinity for the exchange sites (Epstein 1956). The acid soils of the study area, especially those of the ridges, have high levels of exchangeable aluminum (Table 2), and over a wide range of sites, soil calcium is negatively correlated with soil aluminum ($r = -0.505$, significant at the 0.05 level, from present data and that of McColl and Humphreys (1967)). In soils with small amounts of exchangeable calcium and magnesium, phosphorus absorption by roots and phosphorus metabolism within the plants may be inhibited, not only by poor root extension owing to low calcium levels, and by small quantities of soluble phosphorus, but also by accumulation of large amounts of aluminum at the root surfaces which restrict calcium and magnesium absorption. That is, the concentration of phosphorus in the leaves may be dependent, not only on the total phosphorus concentration or the amount of soluble phosphorus in the soil and on the volume of soil penetrated by roots, but also by the interaction of cations at the root surface. Evidence of these combined effects are given in Table 2 (total amounts of soil nutri-

ents, kg/ha) and in Table 3 (tissue concentrations). Although site 1 has more total phosphorus in the profile than sites 2 and 3, the aluminum content is very high and the calcium and magnesium levels are low. The effects (ignoring different species) are shown in Table 3, where leaves from site 1 are much lower in phosphorus concentration than those of sites 2 and 3, even though site 1 has the highest soil phosphorus concentration.

The significant correlations of leaf phosphorus with ratios of soil nutrients (Table 4) are in agreement with the proposed hypothesis. The ratio $P \times \text{Ca}/\text{Al}$, therefore, is called "modified soil phosphorus," being an estimate of phosphorus available to roots for absorption, and for uptake in the plant. There is a reasonable correlation between this ratio in the soil (Table 4), and the concentration of phosphorus in the leaves, and when plotted (Fig. 3), segregation of the species into their respective associations is apparent. Humphreys (1964b) proposed a similar interaction of soil calcium, aluminum and phosphorus in the absorption of phosphorus by *Pinus radiata* D. Don in New South Wales plantations. To increase productivity, he prescribed fertilizer amendments which varied in calcium and phosphorus content according to the nature of the soil in the particular area.

SUMMARY AND CONCLUSIONS

The simplified, idealized diagram of the soil-plant relationship over the topographic gradient

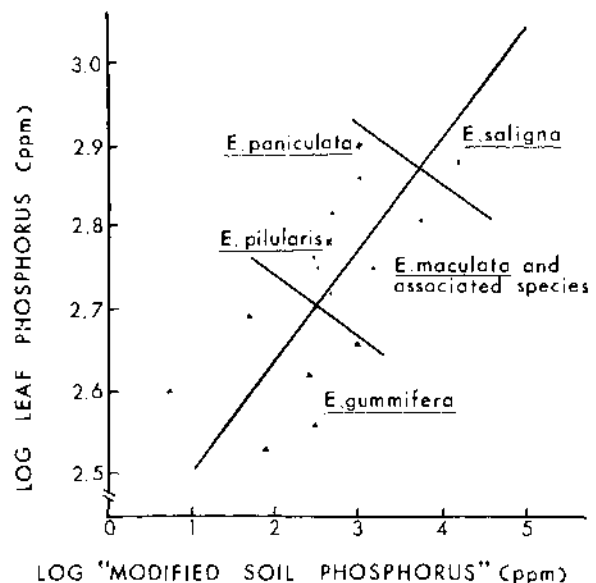


FIG. 3. Relationship of leaf phosphorus of *Eucalyptus* species and "modified soil phosphorus" ($P \times \text{Ca}/\text{Al}$) showing segregation of species associations in Benandra State Forest, New South Wales.

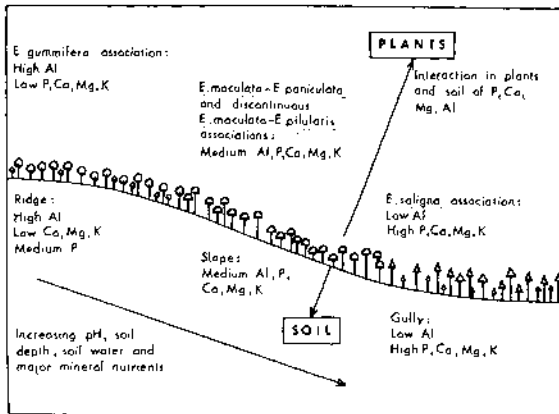


FIG. 4. Idealized diagram of some soil-plant relationships in *Eucalyptus* associations in Benandra State Forest, New South Wales. Total phosphorus and exchangeable cations are indicated for soil.

(Fig. 4) summarizes some of the findings of this investigation.

The ridge site has a high soil bulk density, high stone and sand contents, low soil depth, low levels of important mineral nutrients, and smaller quantities of soil moisture in the "rooting zone." The combination of these factors forms a harsh environment, but one to which the *E. gummifera* association seems well adapted. On the slopes the soil nutrients and moisture regimes become more favorable for plant growth. The deeper soils have higher clay contents, lower bulk densities, higher levels of mineral nutrients, and greater quantities of soil moisture. These better conditions are reflected in taller trees and a trend toward more mesomorphic understory vegetation, with some rainforest species occurring in the *E. saligna* association of the gullies. There is little evidence that moisture or nutrients are particularly critical to growth in the gully site. In years of minimal rainfall, however, soil-moisture may become limiting, especially in the more sandy soils of the ridges.

Soil phosphorus and calcium are also limiting factors. Calcium is concentrated in the bark and wood of trees and usually constitutes more than half of the mineral content of the bark (Kramer and Kozlowski 1960). The greatest reserves of calcium in the species studied here, therefore, appear to be limited by the content in the supporting soil. Logging of the poorer sites would rapidly decrease site quality by the removal of limited amounts of calcium taken up in the wood and bark especially. In addition to soil phosphorus and calcium, other factors may also control distributional patterns and plant growth in the study area. For example, McColl and Humphreys (1967) found nitrogen to be growth limiting to species of the study area.

The interaction of cations and the resulting effect on soil phosphorus availability indicate that more detailed investigations of this aspect might also contribute to an explanation of *Eucalyptus* species distribution and growth.

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THE COMPETITIVE STRUCTURE OF COMMUNITIES: AN EXPERIMENTAL APPROACH WITH PROTOZOA

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Abstract. An empirical test of the existence of higher order interactions was carried out using four ciliate protozoans, *Paramecium caudatum*, *P. bursaria*, *P. aurelia*, and *Blepharisma* sp.

All four ciliates were cultured individually, and their population histories were described quite well by the simple logistic equation.

Attempts to explain minor deviations of the data from the logistic by use of the one or two time lag logistic failed. A more complicated time lag phenomenon must be operative.

Every possible pair of the four ciliates was cultured and a trial and error procedure was used to estimate α and β of the Gause equations. In all cases the simple Gause equations seemed adequately to describe the data.

All four ciliates were cultured together and compared to predictions made by use of the competition coefficients estimated from pair-wise competition and population parameters estimated from single species population growth. The correspondence between prediction and data suggests that the higher order interactions have slight or no effect on the dynamics of this artificial community.

The central goal of community ecology is to understand the dynamics of community organization. Most likely that goal would be best approached from the point of view of mechanism, beginning with basic principles and deducing how communities should behave. However, such attempts have in the past been stifled by certain methodological difficulties, diverting the attention of community ecologists toward more empirical observations. These empirical observations have usually taken the form of measuring the relative

abundance of species (number of species with a given number of individuals).

Most of the work concerned with the latter may be dichotomized as follows. One series of papers (Fisher, Corbet, and Williams 1943; Preston 1948, 1962a, b; Hairston and Beyers 1954; Hairston 1959) emphasizes underlying mathematical distributions and causes of deviance from these distributions. Another series, stimulated by Margalef (1957), and rigorously formalized by Pielou (1966a, b), is concerned with measuring the relative abundance of species, usually to compare communities to each other.

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