Variation in the *Eucalyptus gunnii–archeri* Complex. III*. Reciprocal Transplant Trials

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Abstract

Two multicharacter clines in the more or less continuous stands of *Eucalyptus gunnii–archeri* on the Central Plateau, Tasmania, are genetically based and appear to parallel independent habitat gradients. Results from experimental gardens established near the extremes of each cline suggest that these clines are at least partly maintained by spatially varying selective forces. Spatial variation in population fitness could be partly attributed to a differential response to drought, frost and insect predation.

Most characters associated with extension growth (e.g. height, internode length, leaf size) exhibited marked phenotypic plasticity. In contrast, several characters of taxonomic importance in the complex, and which vary markedly between populations (e.g. seedling leaf shape, glaucousness), exhibited little environmental modification. The ontogenetic pattern varied between populations and, for many characters, the direction of environmental modification was the same as the direction of genetic differentiation.

Introduction

Two major genetically based clines occur in the more or less continuous stands of *Eucalyptus gunnii–archeri* on the Central Plateau, Tasmania (Potts and Reid 1985a, 1985b). These multicharacter clines appear to parallel independent habitat gradients and encompass a large portion of the variation in the *E. gunnii–archeri* complex. A north–south cline occurs between subsp. *archeri* (sens. Pryor and Johnson 1971) and subsp. *gunnii* (sens. Pryor and Johnson 1971; i.e. '*divaricata*' morph, Potts and Reid 1985a) and is associated with the transition from a subalpine, mixed eucalypt/rainforest or closed scrub habitat on the northern scarp of the Western Tiers to the open woodland habitat bordering the extensive 'frost hollows' around Great Lake. Interacting with this cline is another major cline associated with variation in exposure to the alpine environment which achieves maximum expression along an altitudinal transect running approximately east–west. This transect encompasses phenetic extremes of the altitudinal cline within the complex as well as the clinal transition between forms classified as *E. divaricata* and *E. gunnii* by Brett (1938) (i.e. '*divaricata*' and 'southern *gunnii*' morphs, Potts and Reid 1985a).

Experimental gardens established near the extremes of each major cline provide an indication of the selective differential between extreme populations as well as a biological assay of site characteristics. The main factors limiting seedling growth are discussed and the magnitude of the plastic response in a range of morphological characters is assessed.

Materials and Methods

Two-year-old seedlings (from progeny trial 1, Potts and Reid 1985b), hardened outdoors at Hobart, were transplanted in April 1979 into experimental gardens at Liawenee (LH, 1150 m), Shannon Lagoon (SL, 1050 m), Pensford (PF, 960 m) and Projection Bluff (P2, 1100 m). (Site locations are detailed in

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Potts and Reid 1985*a*.) Six populations were included in each trial representing subsp. *archeri* (P1, P2) and subsp. *gunnii* ['*divaricata*' — LH, SL and 'southern *gunnii*' — PF, SP (Snug Plains) morphs, Potts and Reid 1985*a*]. The Liawenee and Pensford populations are taken as extremes of the altitudinal gradient (i.e. the southern Plateau transect), and the subsp. *archeri* populations (P1, P2) and the population from Shannon Lagoon (SL) represent extremes of the north–south cline (i.e. Pine Lake transect, see Potts and Reid 1985*a*, 1985*b*). At each site 12 seedlings from each population were planted in two 6 × 6 Latin squares, placed end-to-end and surrounded by an edge row. Seedlings were planted 1 m apart and, as far as possible, each mother was represented once per square, being randomly assigned to a population position. Each garden was fenced and the only site treatment involved the removal of shrub cover where necessary (i.e. P2 and LH).

Characters Scored

Assessments of survival and growth were made regularly over a 5-year period (to April 1984). Seedlings appearing dead at the time of scoring were classified as such regardless of whether regeneration occurred later from lignotuber or epicormic buds. Height was measured from ground level to the maximum vertical height of the living portion of the plant, and stem diameter (Sept. 1981) was measured at the cotyledonary node. Height and stem diameters were expressed as the increment from the corresponding measure prior to planting (i.e. $\triangle H$ and $\triangle D$). The basal area (Dec. 1982, Mar. 1984) of each surviving seedling was calculated by measuring the diameter of all living stems at 10 cm above ground level.

Estimates of the percentage of the leaf area damaged by frost were obtained approx. 2 months after planting, following the method of Ashton (1958). For each leaf, the fraction of leaf area killed was estimated to the nearest quarter and the total damage estimated from the number of leaves in each category. The low temperature response of populations was also examined in an artificial frost using a cold-room. Glasshouse-grown seedlings were preconditioned for 2 weeks (8°C day / 3°C night, 9 h photoperiod) then subjected to 3 h at -7°C after insulating roots with a layer of vermiculite. Seedlings were then returned to the glasshouse and 1 week later leaf damage was scored as previously described.

The percentage of the leaf area produced over the 1980–81 growing season that was lost through direct insect grazing (% insect grazing) or due to necrosis (% necrotic) was estimated (Sept. 1981) in a similar manner to frost damage, although in this case single leaf estimates were made to the nearest half. The percentage of leaves occurring on lignotuberous shoots as opposed to the main stem was used as an estimate of the relative vigour of the main stem and as an indication of seedling habit (% leaves lig / tot). The percentage of leaf area lost from the 1979–80 season's growth due to insect grazing was subjectively evaluated. Seedlings were scored for the presence or absence of a petiole and intranode (Feb. 1981), and later (Sept. 1981) the maximum intranode length and corresponding internode length were measured. A single representative leaf from the area of maximum summer growth was collected (Sept. 1981) from each seedling and the dimensions, indicated by Potts and Reid (1985*b*), as well as petiole length (PET) were measured. Glaucousness was scored on a 5 class scale from green (0) to highly glaucous leaves and stems (4). Estimates of population variation in lignotuber development were obtained from seedlings prior to planting experimental gardens (see Potts and Reid 1985*b*). Lignotuber development was quantified by obtaining the difference in diameter measured across the cotyledonary lignotubers (L) and the stem diameter perpendicular to the latter measurement (D), and the differences expressed relative to the cotyledonary stem diameter (D) [i.e. $(L-D)/D$; see Ladiges and Ashton 1974].

Insect Predation and Collections

Phytophagous insects were collected from the foliage of mature *E. gunnii–archeri* trees surrounding each garden over the 1979–80 (Nov.–Apr.) and 1980–81 (Jan.–Feb.) growing seasons. Samples were collected from at least 10 trees at each site using an insect net and taking a total of 25 sweeps of the foliage per site. The bias associated with this sampling method is discussed by Morrow (1977). Collections were sorted into species groups and tentatively identified by Dr J. Madden (Faculty of Agricultural Science, University of Tasmania).

Statistical Analysis

For surviving seedlings, growth and morphometric data were subject to analysis of variance (ANOVA–model 1). Between squares as well as row and column effects within squares were initially

removed from the error term. However, these effects were generally small and were pooled with the error variance in the analyses presented. Percentage data were angular-transformed prior to ANOVA and, unless otherwise indicated, back-transformed results are presented (see Sokal and Rohlf 1981). The variation between populations within sites was examined using both one-way ANOVA and the non-parametric Kruskal–Wallis test (Sokal and Rohlf 1981). Where an ANOVA was significant, the l.s.d. procedure (Sokal and Rohlf 1981) was used to indicate significant population differences. Frequency data were tested by the χ^2 test for association, and for this purpose populations were pooled into 'archeri' (P1 + P2), 'divaricata' (LH + SL) and 'southern *gunnii*' (PF + SP) ($n = 24$) due to the low number of replicates in each population. While this grouping of populations corresponds to the phenetic classification given by Potts and Reid (1985*a*), populations form a clinal series (e.g. LH, SL, PF, SP; Potts and Reid 1985*a*, 1985*b*) and there are clearly significant genetic differences between populations within each grouping.
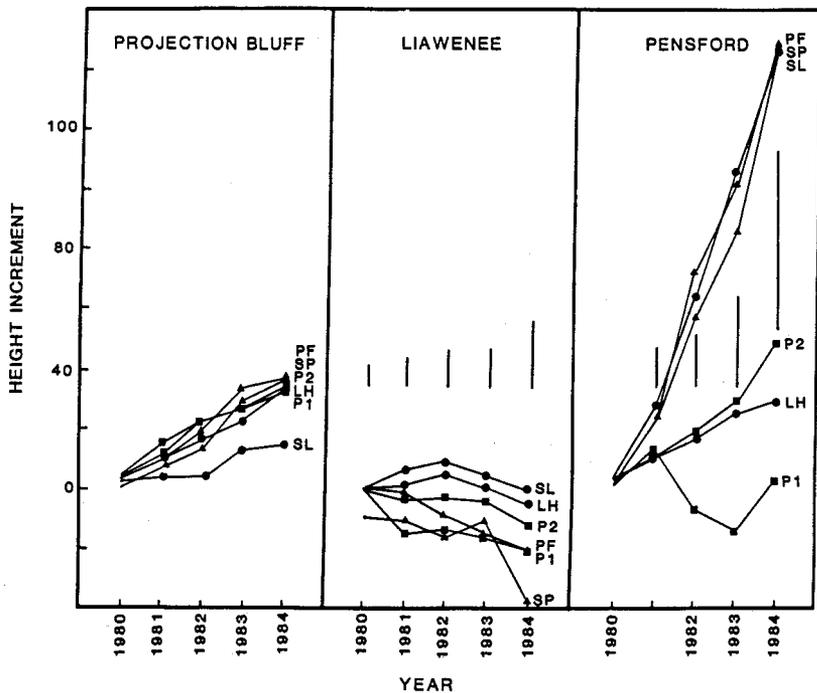

Fig. 1 Mean height (cm) increments for 'archeri' (P1 and P2; ■), 'divaricata' (LH and SL; ●) and 'southern *gunnii*' (PF and SP; ▲) populations in experimental gardens. Increments are calculated from height prior to planting and, where the ANOVA for the difference between populations at a given time is significant ($P < 0.05$), the l.s.d. 0.05 (based on $n = 12$) is shown. Data are not presented for the Shannon Lagoon site due to the low replication in the later phase of the trial.

Results

Seedling Growth and Mortality

Significant differences ($P < 0.001$) in the number of surviving seedlings were evident between sites and between populations pooled over sites. The latter results from high, differential mortality of subsp. *archeri* (P1 and P2) seedlings at the subsp. *gunnii* sites (LH, SL and PF; Table 1), the main causes of which are discussed later. For surviving seedlings, the environmental (site) component of variation in growth characteristics (Table 2) is large, and for height, increases with time. The population differences in growth rate noted by Potts

and Reid (1985*b*) are partly maintained, although the population × site interactions are highly significant ($P < 0.001$) after the initial establishment phase. The latter is partly due to a tendency for populations to grow comparatively better at sites most similar to their site of origin. This is exemplified by the average increment in height (Fig. 1) and diameter, average height (Fig. 2) and basal area of surviving seedlings.

Sites at either extreme of the Pine Lake transect differ markedly ($P < 0.001$) in the probability of seedling survival for all genotypes, whereas there was virtually no difference between extremes along the altitudinal gradient of the southern Plateau transect (Table 1). The 'frost hollow' site at Shannon Lagoon was the most severe of all sites for establishment of seedlings regardless of their origin. By the third year, virtually all seedlings from populations P1, P2 and SP were dead as well as 50% or more of the seedlings from the remaining subsp. *gunnii* populations (LH, SL and PF) (Table 1). This contrasts with the Projection Bluff site (P2) where after 4 years only two seedlings were dead. There is evidence for strong
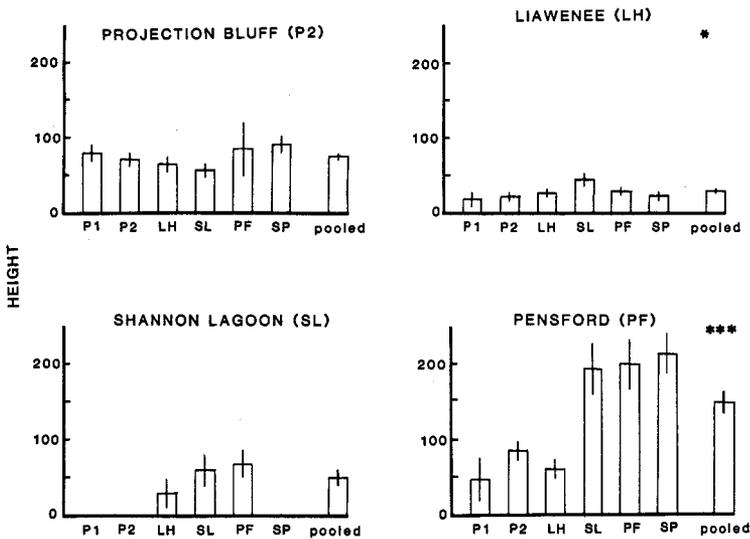

Fig. 2. Mean (± s.e.) height (cm) for surviving seedlings in the experimental gardens 5 years after planting. All populations for which $n < 3$ have been excluded (i.e. populations P1, P2 and SP from Shannon Lagoon) and any significant difference between populations at each site is indicated: * $P < 0.05$; *** $P < 0.001$.

selection against the subsp. *archeri* seedlings at the Shannon Lagoon site, with the elimination of the P1 seedlings in particular being the most rapid (Table 1). While there is greater survival of seedlings from the local populations at the Shannon Lagoon site (SL, 1982-84, Table 1) this is not significant, and in terms of survival and growth there is no evidence for a selective response differentiating the subsp. *gunnii* populations LH, SL and PF at this site.

At the subsp. *archeri* site, there is a trend for seedlings from the Shannon Lagoon site to exhibit the poorest growth (e.g. Figs 1–3). However, this was, at most, marginally significant ($P < 0.05$) and there was no significant difference between the subsp. *archeri* and the other subsp. *gunnii* (PF, SP and LH) populations. Nevertheless, the growth of these last populations was significantly ($P < 0.001$) reduced when compared to their relative performance at the Pensford site (e.g. Figs 1–3) and in terms of both survival and growth the subsp. *archeri* seedlings are clearly more competitive at their local site (P2) than at any other.

Table 1. Seedling deaths in experimental gardens (n = 12)

The number of plants showing drought damage in March 1980 are in parenthesis. Significance of the χ^2 test for association between mortality and cluster type is indicated (a) 'archeri' v. 'divaricata' v. 'southern gunnii'; (b) 'divaricata' v. 'southern gunnii'. * $P<0.05$; ** $P<0.01$; *** $P<0.001$; n.s., not significant

Population	Seedling deaths					
	Nov. 1979	Mar. 1980	Sept. 1981	Apr. 1982	Apr. 1983	Mar. 1984
Site: Projection Bluff (P2)						
P1	0	0	0	0	0	0
P2	0	0	1	1	1	1
LH	0	0	0	1	1	1
SL	0	0	0	0	0	1
PF	0	0	0	0	0	0
SP	0	0	0	0	0	0
(a)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
(b)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Site: Liawenee (LH)						
P1	1	1	2 •	4	7	6
P2	2	2	3	4	4	5
LH	0	0	0	1	1	1
SL	0	0	0	1	1	1
PF	1	1	1	2	3	4
SP	0	0	1	3	4	4
(a)	n.s.	n.s.	n.s.	n.s.	*	*
(b)	n.s.	n.s.	n.s.	n.s.	n.s.	*

Population	Seedling deaths					
	Nov. 1979	Mar. 1980	Sept. 1981	Apr. 1982	Apr. 1983	Mar. 1984
Site: Shannon Lagoon (SL)						
P1	1	8(7)	8	12	12	12
P2	0	5(5)	6	10	11	11
LH	0	0(6)	2	6	9	8
SL	0	2(5)	2	5	7	7
PF	0	3(6)	4	7	8	8
SP	0	3(6)	4	11	11	11
(a)	n.s.	**	*	**	*	*
(b)	n.s.	n.s.	n.s.	*	n.s.	n.s.
Site: Pensford (PF)						
P1	0	0	7	8	9	10
P2	0	0	4	4	4	5
LH	0	0	1	1	2	2
SL	0	0	2	2	2	2
PF	0	0	1	2	2	2
SP	0	1	3	3	3	3
(a)	n.s.	n.s.	*	**	**	***
(b)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Table 2. Two-way analysis of variance (model 1) for growth and morphological characters

The d.f.s for the full design are shown (residual d.f. = 264) but, due to mortality, orthogonality was not maintained for the majority of characters (see Table 1). Morphological characters (detailed in Potts and Reid 1985b): LL, lamina length; LW, lamina width; LWP, distance from the base to the widest point; PET, petiole length; BASE, EMARG, degree of cordateness and emarginateness; INTER, internode length; INTRA, intranode length; GLAUC, glaucousness. PC1, PC2, PC3, the first three principal components derived from PCA (TOT, CORR; Fig. 10) of five leaf characters (LL, LW, LWP, BASE, EMARG). Significance of each component is indicated: *P = 0·05; ** P = 0·01; *** P = 0·001; n.s., not significant

	Effects		
	Site d.f. = 3	Population d.f. = 5	Site × Pop. d.f. = 15
Growth characters			
Height			
Apr. 1979 (start)	n.s.	***	n.s.
Mar. 1980	**	***	n.s.
Sept. 1981	***	***	***
May 1982	***	***	***
Apr. 1983	***	***	***
Mar. 1984	***	***	***
Δ Height			
Mar. 1980	n.s.	**	**
Sept. 1981	***	**	**
May 1982	***	**	***
Apr. 1983	***	***	***
Mar. 1984	***	**	***
Diameter 1981	***	**	***
Basal area			
Dec. 1982	***	***	***
Mar. 1984	***	***	***
Percentage of:			
Frost damage 1979	*	***	n.s.
Insect damage 1981	***	n.s.	***

	Effects		
	Site d.f. = 3	Population d.f. = 5	Site × Pop. d.f. = 15
Percentage of:			
Necrotic damage 1981	***	***	***
Total damage 1981	***	*	***
Lig/Tot leaves 1981	***	***	n.s.
Total leaves 1981	***	*	***
Morphological characters			
LL	***	***	***
LW	***	***	**
LWP	***	***	***
PET	**	***	***
BASE	*	***	n.s.
EMARG	n.s.	***	n.s.
LL/LW	n.s.	***	*
LL/LWP	n.s.	***	*
PC1	***	***	***
PC2	n.s.	***	n.s.
PC3	n.s.	**	n.s.
INTER	***	***	**
INTRA	***	***	**
GLAUC	*	***	n.s.

The difference in seedling mortality between the subsp. *gunnii* sites near the altitudinal extremes (LH *v.* PF) is small and there is even an initial trend for survival to be greater at the highest altitude site (LH: 1981, 1982; Table 1). This mainly resulted from high differential mortality of the subsp. *archeri* (P1 and P2) seedlings at the Pensford site over the 1981 winter (Table 1). Nevertheless, the Pensford site (PF) and Liawenee (LH) sites are clearly differentiated ($P < 0.001$) in terms of productivity (e.g. height, basal area). For all populations there is a marked reduction in both height (e.g. Fig. 1) and stem diameter increment at the latter site, although the relative magnitude of the reduction in height (Figs 1 and 2) and basal area (Fig. 3) is less for LH than for the other subsp. *gunnii* populations (SL, PF and SP). At the Liawenee site, there is a tendency (1985, $P < 0.05$) for greater seedling mortality in the low altitude populations of subsp. *gunnii* (PF and SP, Table 1). Furthermore, the surviving seedlings (PF and SP) were less vigorous than seedlings from higher altitude populations (LH and SL, Fig. 1). The total basal area of seedlings from the Liawenee population is greater than either of the subsp. *archeri* populations (P1 and P2, Fig. 3) and later scorings indicate a greater mortality of subsp. *archeri* seedlings at this site ($P < 0.01$, Table 1). These results clearly suggest that the highest altitude population (LH)
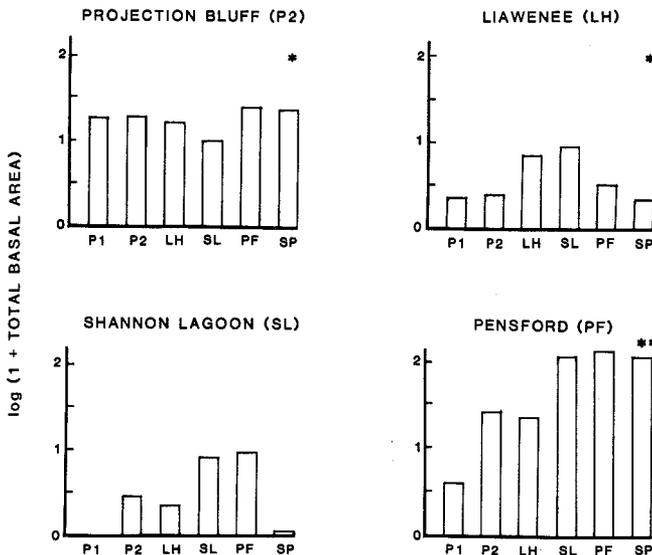

Fig. 3.   The total basal area (cm^2) of seedlings from each population 5 years after planting. Significant differences between populations in the average basal area of surviving seedlings are indicated:
$* P < 0.05$; $** P < 0.01$.

is most competitive, if not at a selective advantage (except for SL), at its own site. It also performs comparatively well at the subsp. *archeri* site (P2) but is surpassed in growth at the low altitude site at Pensford by the other subsp. *gunnii* populations (SL, PF and SP), which are rapidly dominating surviving seedlings from all other populations (Figs 1-3). While there is some indication of greater basal area of the Pensford seedlings at their local site (Fig. 3), this is not significant for the average basal area of surviving seedlings or for other growth measures (Figs 1 and 2). To date there is no evidence for a difference in survival or growth between the subsp. *gunnii* populations (SL, PF amd SP) at the Pensford site. The data suggest that the Shannon Lagoon population (SL) is competitive with populations from both higher (LH) and lower (PF) altitudes at their local site. However, rather than resulting from a broad environmental range, this is more likely to reflect the intermediate status of the population along the exposure cline and suggests a degree of concordance between morphology and the physiological response.

   In terms of the growth of surviving seedlings, sites broadly rank in the order Pensford (PF), Projection Bluff (P2), Shannon Lagoon (SL) and Liawenee (LH) (e.g. Figs 1-3), with the best growth generally occurring at the low altitude site at Pensford (PF). At the highest

altitude (LH) and open woodland (SL) sites there is effectively a reduction in seedling height (Fig. 1) due to the death of all or part of the main stem on many seedlings and subsequent regeneration from lignotuberous or epicormic buds. This mainly resulted from the cumulative effects of frost (Fig. 4), drought (Tables 1 and 3) and insect predation (Fig. 5), the
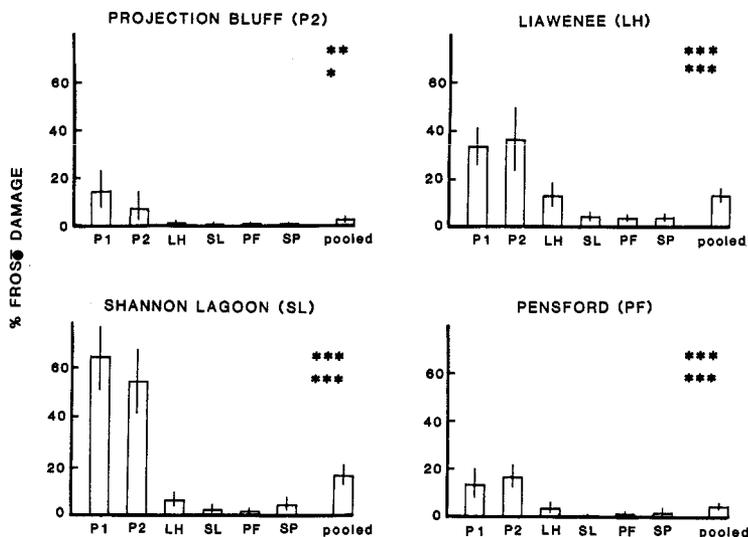

Fig. 4. Mean (± s.e.) percentage of leaf area damaged by frost 2 months after planting. Results have been back-transformed from angular-transformed data and the significance of the difference between populations based on ANOVA (*top*) and the Kruskal-Wallis test (*bottom*) is indicated: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

Table 3. Percentage of surviving plants at each site exhibiting drought damage in March 1980 and 1981

The significance of the χ^2 test for association is indicated *** ($P = 0.001$) and the number of surviving seedlings is shown in Table 1

Site	March 1980	March 1981
P2	0	0
LH	0	2·9
SL	45·8	18·1
PF	5·7	1·4
	***	***

effects of which were frequently differential and varied between sites (Table 2). Reduced vigour of the main stem and a shift toward the lignotuberous multistemmed habit were most apparent at Shannon Lagoon and Liawenee (Fig. 6). In contrast, at the low altitude site at Pensford new growth was virtually confined to axillary buds on the main stem. These plastic differences in apical dominance and tree height accord with the difference in canopy height and habit between high (LH) and low (PF) altitude subsp. *gunnii* sites on the Central Plateau and, while genetic differences between populations are in a similar direction, there is clearly a large environmental (site) component to both height and habit (Table 2).
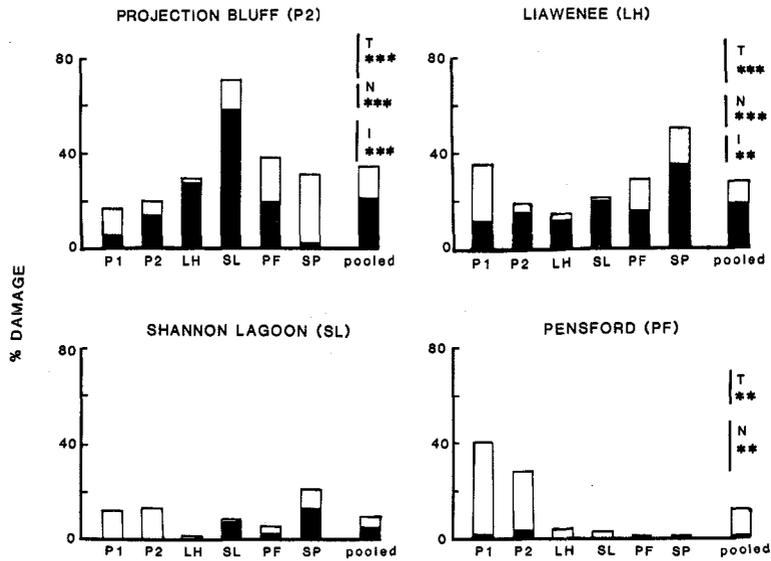
Fig. 5. The mean percentage of the leaf area expanded in the 1980–81 growing season which was lost through insect grazing (shaded) or necrosis. The cause of necrotic damage was not identified. l.s.d. 0·05 bars (based on $n = 12$) for the total (*T*), insect (*I*) and necrotic (*N*) damage are indicated where comparisons between populations are significant: ** $P < 0·01$; *** $P < 0·001$.
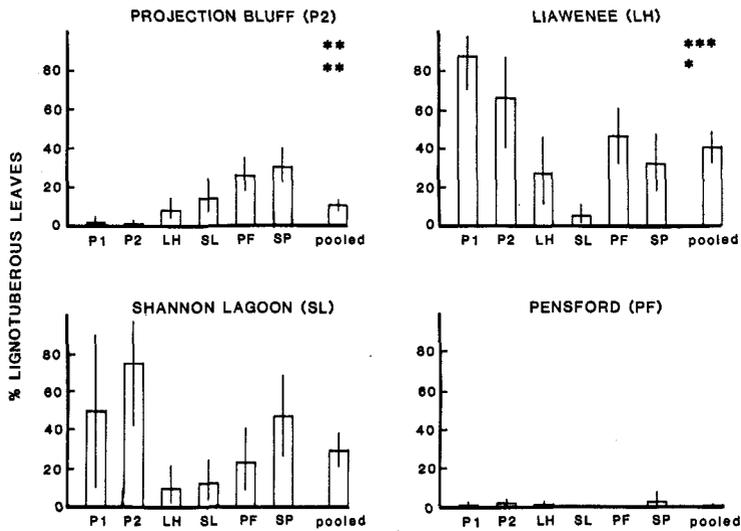
Fig. 6. The mean ($\pm$ s.e.) percentage of the total number of leaves expanded in the 1980–81 season which occurred on lignotuberous shoots. Results have been back-transformed from angular-transformed data. Significant differences between populations based on ANOVA (*top*) and Kruskal–Wallis test (*bottom*) are indicated: * $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.

In view of the extreme nature of the 'frost hollow' habitat, it is possible that the divaricating branching pattern of the '*divaricata*' form (see Brett 1938) is partly a result of crown damage and frequent regeneration from epicormic buds. Furthermore, it is noteworthy that the genetic potential for lignotuber development is greatest in seedlings from this site (i.e. SL, Fig. 7). In contrast, lignotuber development was least in seedlings from the mixed eucalypt/rainforest and closed scrub habitat beneath Projection Bluff (i.e. P1 and P2, Fig. 7), where the probability of seedling survival was greatest. This accords with the trend observed in other eucalypt species (e.g. Ladiges and Ashton 1974; Ashton 1981) for an increase in lignotuber development in areas prone to frequent drought and fire such as "open forest, woodlands and 'tree-heath' environments".
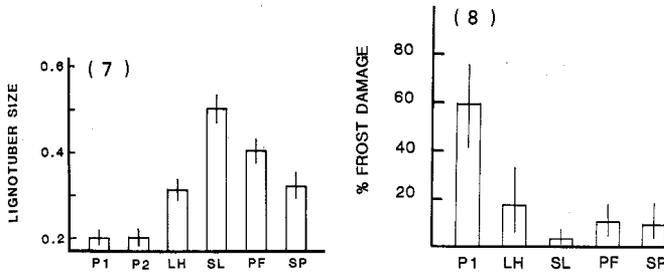

Fig. 7. The mean ($\pm$ s.e.) lignotuber size [$(L-D)/D$, see Methods] of populations when grown in a common environment.
Fig. 8. The mean ($\pm$ s.e.) percentage of leaf area damaged after an artificial frost of $-7°C$. The results have been back-transformed from angular-transformed data. No. of seedlings: P1, 7; LH, 8; SL, 8; PF, 8; SP, 8.

Factors Affecting Seedling Survival

Frost

Frost damage was first observed on plants 1–2 weeks after planting, following a cold snap with below freezing temperatures accompanied by high winds and snowfall. Frost damage was assessed 2 months after planting (July 1979) when minimum temperatures ranged from $-3\cdot8$ to $-6°C$ (i.e. P2 $-4°$, LH $-4°$, SL $-6°$, PF $-3\cdot8°$), with the lowest temperature occurring at the 'frost hollow' site at Shannon Lagoon.

Significant differences ($P < 0\cdot001$) in the proportion of leaf area damaged were apparent between sites and populations (Table 2). The greatest frost damage occurred at the 'frost hollow' (Shannon Lagoon) and high altitude subsp. *gunnii* sites and the least at the subsp. *archeri* site beneath Projection Bluff (SL > LH > PF > P2) (Fig. 4). The greatest frost damage observed at the site at Shannon Lagoon was indicative of a general trend over the full experimental period for lower minimum temperatures to be recorded at this site (Potts, unpublished data). Higher maximum temperatures were usually also recorded at this site, suggesting that seedlings are subject to greater temperature extremes than at other sites. At all sites, significantly ($P < 0\cdot01$) greater frost damage occurred to the subsp. *archeri* (P1 and P2) seedlings than to those of the subsp. *gunnii* populations, whereas there was no significant difference between the subsp. *gunnii* populations (Fig. 4). Similar results ($P < 0\cdot05$) were observed following an artificial frost of $-7°C$ (Fig. 8). Few seedlings in the experimental gardens were killed by frost and, where damage was heavy (e.g. Shannon Lagoon), seedlings usually recovered from lignotuber or epicormic buds.

Drought

Drought as opposed to frost, was the major cause of seedling mortality at the Shannon Lagoon site. Over the two summers during which the gardens were intensively monitored (1979–80; 1980–81), marked drought damage occurred only at the open woodland site at

Shannon Lagoon (Table 3). The open nature of this habitat results in full exposure to both the late afternoon sun and the desiccating effects of hot, dry north-west winds. In both years water stress was apparent at the beginning of February, whereas early in the season seedlings exhibited relatively vigorous growth. Death due to drought damage during the 1979–80 summer was differential, with the subsp. *archeri* seedlings being less drought tolerant (Table 1). For these seedlings, death from drought (in 1979–80) was not associated with the degree of frost damage the previous winter. Drought, therefore, appears to be a separate selective effect against the subsp. *archeri* seedlings in the open woodland habitat.
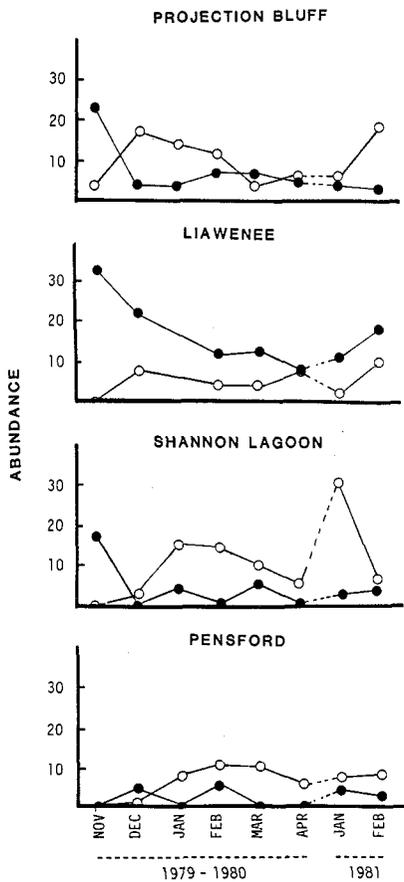
Fig. 9. The abundance (number) of Coleoptera (● leaf-eating) and Homoptera (○ sap-sucking) insects in samples collected from adult foliage at each site.

Insect predation

   The samples from adult trees and observations of seedlings in the experimental gardens clearly indicate that the four sites are highly differentiated with respect to the local phytophagous insect fauna (Fig. 9; Table 4). Differences between sites were both qualitative and quantitative with large differences occurring in the relative abundance of Coleoptera (leaf-eating; mainly Chrysomelidae and Scarabidae) and Homoptera (sap-suckers; mainly Psyllidae) insects (Table 4). The activity of leaf-eating insects was greater at higher altitudes (e.g. LH, P2) in terms of both insect abundance and damage to seedlings (Figs 5 and 9; Table 4). This is particularly so at the highest altitude site (LH) where continuous heavy grazing (mainly by a single *Trachymelid* species) of seedlings and adults resulted in considerable loss of leaf area (e.g. Fig. 5; Table 4) and damage to apices.

The proportion of leaf area lost from a single season's growth through direct insect grazing was large at several sites (PB, LH) and exceeded losses associated with leaf necrosis arising from a variety of factors [e.g. drought, frost, fungal and other forms of insect (e.g. cocoons) damage] (Fig. 5). Leaf-eating insect activity was low at the subsp. *gunnii* sites at Pensford and Shannon Lagoon (e.g. Figs 5 and 9; Table 4) where sap-sucking species predominate. The absence of such grazing at the Pensford site in particular may partly contribute to the generally high growth rates at this site (e.g. Figs 1–3). In sites where insect grazing was high (LH and P2), there is some evidence for preferential grazing of seedlings from specific populations (e.g. Table 2, Fig. 5; site P2, population SL; site LH, population SP).

Table 4. **Summary of insect data collected from adult trees and observed (1980–81) on seedlings in the experimental gardens**

Abundance data refer to the number of individuals collected or observed

	P1	LH	SL	PF
	Adult samples			
Mean abundance of Coleoptera per sample (s.e)	6·9(2·4)	15·1(2·9)	4·3(1·8)	2·5(1·0)
Mean abundance of Homoptera per sample (s.e.)	10·0(1·9)	4·5(1·3)	10·1(3·4)	7·1(1·2)
Number of Coleoptera species	8	4	9	7
Number of Homoptera species	10	8	7	8
Total number of species	18	12	16	15
Shannon–Weiner Diversity Index	2·46	1·28	1·95	2·28
	Experimental gardens			
Mean percentage of leaf area				
eaten on new growth: 1979–80	19·50	6·70	1·30	3·90
1980–81	21·10	18·20	4·40	3·90
Abundance of Homoptera per seedling	10·00	0·40	3·90	0·60
Abundance of Coleoptera per seedling	0·00	0·40	0·10	0·00
Proportion of plants on which Homoptera observed	0·86	0·15	0·37	0·22
Proportion of plants on which Coleoptera observed	0·00	0·19	0·04	0·00

Genetic and Plastic Components to Character Variation and Ontogenesis

The present study indicates a large plastic response in characters which are influenced by or reflect plant vigour (e.g. internode length, lamina size, height, habit; see Table 2) and large treatment effects are frequently reported for such characters in *Eucalyptus* (e.g. Clucas and Ladiges 1979; Davidson and Reid 1980). In contrast, other characters such as glaucousness and those associated with leaf shape exhibit relatively little environmental modification (e.g. Table 2) and this is also evident in the data of Clucas and Ladiges (1979). Variation in lamina size and shape was separated by principal components analysis (PCA) (see Table 2; Fig. 10). The first principal component (PC1, 55%) mainly reflects lamina size, whereas later components mainly incorporate facets of lamina shape (PC2, 30%; PC3, 12%). ANOVA (Table 2) clearly demonstrates that a remarkably low level of plasticity is associated with the leaf shape components, which is particularly significant as, along with glaucousness, adult and seedling leaf shape are important characters differentiating subspecies. In contrast, there is a large plastic (site) component to leaf size, although the population and interaction components are still highly significant ($P < 0·001$). This is mainly due to genetic differences in leaf size between the '*divaricata*' and 'southern *gunnii*' seedlings and, despite considerable variation between sites, the three phenetic clusters can still

be distinguished in the PCA ordination (Fig. 10). Plasticity in leaf size appears to be mainly associated with plant vigour, with both leaf size and plant vigour decreasing at the Liawenee and Shannon Lagoon sites. This supports the previous suggestion (Potts and Reid 1985*b*) that genetic differentiation in juvenile leaf size along the altitudinal cline may be partly a pleiotropic effect of genetic variation in growth rate.
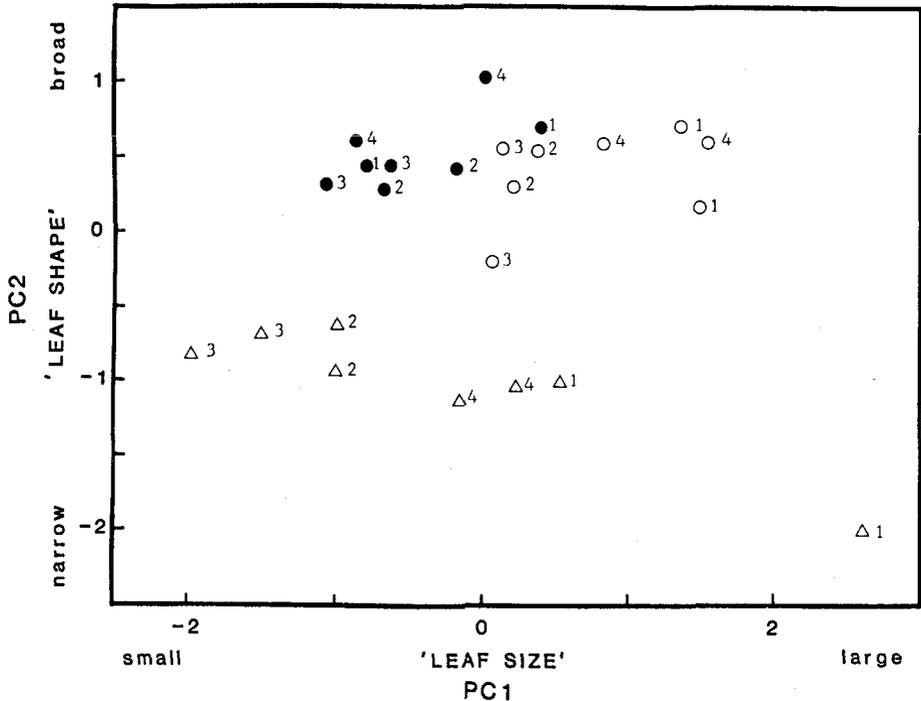

Fig. 10. Principal component ordination (PC1 *v.* PC2) derived from analysis of seedling leaf characters. The plot shows '*archeri*' (P1, P2 △), '*divaricata*' (SL, LH ●) and 'southern *gunnii*' (PF, SP ○) sample means in each experimental garden. 1, Projection Bluff, P2; 2, Liawenee, LH; 3, Shannon Lagoon, SL; 4, Pensford, PF. PC1 and PC2 describe variation mainly reflecting variation in leaf size and leaf shape respectively.

There are significant, genetically based, differences between populations in the pattern of ontogenetic development. The transition from the juvenile to adult foliage involves a continuous sequence with leaves becoming narrower (i.e. lanceolate), isobilateral, alternate and petiolate with maturity. There is clearly a trend from the '*archeri*', 'southern *gunnii*' to the '*divaricata*' morph, for development of the adult foliage type to be ontogenetically delayed. This trend is clearly exemplified by comparisons (Table 5) at sites where the heights of specific populations are similar (e.g. Pensford and Projection Bluff, see Fig. 2), and has been noted before (Potts and Reid 1985*b*). The frequency of plants exhibiting mature characteristics such as intranodes or petioles is significantly less at both the Liawenee and Shannon Lagoon sites (Table 5). Again, this site variation appears to be associated with plant vigour, although only partly through the reversion associated with regeneration from lignotubers or epicormic buds, as similar significant trends are evident when only undamaged plants are considered (Table 5). As noted previously for other characters, genetic variation in ontogenetic development occurs in a similar direction to the plastic response (Table 5; Potts and Reid 1985*b*). For example, seedlings grown from the most extreme sites and those in which the general expression of mature characters is environmentally delayed (LH, SL) retain the juvenile foliage type longer than other populations (P1, P2, PF and SP) in a common environment.

There is also evidence for genetic variation between populations in the time and vegetative phase at which seedlings reach reproductive (cf. vegetative) maturity. For example, after 5 years, flowering buds were apparant only at the Pensford site and virtually all of the mature individuals were from the low altitude, mallee population which grows on the button-grass plain at Snug Plains. In addition, at least at the population level, there appears to be a degree of ontogenetic independence between characters, and while the early development of adult type foliage coincides with early reproductive maturity in the Snug Plains population this is clearly not the case for the subsp. *archeri* populations. The whip-stick mallee habit of the Snug Plains population is relatively unusual for the subsp. *gunnii* and is maintained

Table 5. Proportion of seedlings with petioles and intranodes for the total number of surviving and undamaged seedlings

Populations are grouped into '*archeri*' (P1, P2), '*divaricata*' (LH, SL) and 'southern *E. gunnii*' (PF, SP) morphs. The significance of the χ^2 test for association is indicated: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s., not significant

	Surviving seedlings			Undamaged seedlings		
	Petiole	Intranode	n	Petiole	Intranode	n
		Projection Bluff (P2)				
P1 + P2	0·91	0·65	23	0·90	0·71	21
LH + SL	0·04	0·04	24	0·08	0·08	13
PF + SP	0·50	0·42	24	0·57	0·48	21
Total	0·48	0·37	71	0·58	0·47	55
	***	***		***	***	
		Liawenee (LH)				
P1 + P2	0·32	0·05	19	0·86	0·14	7
LH + SL	0·04	0·13	24	0·05	0·14	21
PF + SP	0·30	0·43	23	0·36	0·57	14
Total	0·21	0·21	66	0·29	0·29	42
	*	**		***	*	
		Shannon Lagoon (SL)				
P1 + P2	0·30	0·10	10	1·00	0·33	3
LH + SL	0·05	0·05	19	0·06	0·00	17
PF + SP	0·53	0·35	17	0·64	0·43	14
Total	0·28	0·17	46	0·38	0·21	34
	**	*		***	*	
		Pensford (PF)				
P1 + P2	0·67	0·63	24	0·75	0·50	12
LH + SL	0·05	0·27	22	0·05	0·29	21
PF + SP	0·65	0·45	20	0·68	0·47	19
Total	0·45	0·45	66	0·44	0·40	52
	***	n.s.		***	n.s.	
Between gardens	***	***		**	***	

by frequent wildfires which result in the death of stems and subsequent vegetative regeneration from lignotuberous shoots. The precocious flowering in this population is probably an adaptation to the high fire frequency associated with the sedge community, allowing the development of an aerial seed bank in the short fire-free interval.

Discussion

The growth and mortality data presented suggest a close adaptive response of the *E. gunnii–archeri* populations to the local environment. This is common in *Eucalytpus* (Pryor 1959b, 1976; Pryor and Johnson 1971) and is well recognized at the species level (e.g. Moore 1959; Parsons and Specht 1967; Parsons 1968, 1969; Ashton 1976, 1981) and the popu-

lation level (e.g. Barber 1955, 1965; Barber and Jackson 1957; Pryor 1957, 1976; Ladiges and Ashton 1974; Anderson and Ladiges 1978, 1982; and others). Differences in fitness are demonstrated between extreme morphs along the major clines on the Central Plateau, suggesting that selection is a significant factor in maintaining genetic differentiation in the more or less continuous stands. Further evidence includes the facts that (1) the clines appear correlated with variation in habitat and (2) a degree of parallelism is evident in the variation pattern shown by other species (Barber 1955; Potts and Reid 1985a). Nevertheless, it has been argued (Potts and Reid 1985b) that the cline along the Pine Lake transect, between subsp. *gunnii* and subsp. *archeri*, represents a partially stabilized zone of secondary intergradation. This interpretation is clearly not incompatible with the demonstration of selective differentials between extreme morphs, although unfortunately no data are available for intermediate morphs and sites. Differences in fitness between populations are associated with biotic and abiotic factors. Drought and frost sensitivity appear to be the main factors restricting subsp. *archeri* ('*archeri*' morph sens. Potts and Reid 1985a) and there is clearly strong selection against this morph in sites currently occupied by the subsp. *gunnii* populations. However, some evidence suggests that different facets of the environment are limiting the growth of the subsp. *archeri* seedlings at the different subsp. *gunnii* sites. For example, drought was clearly not the cause of the differential mortality ($P < 0.001$) of the subsp. *archeri* seedlings at the Pensford site, which occurred over the 1981 winter. Furthermore, these deaths did not appear to be the direct result of frost damage, but were possibly associated with fungal attack or waterlogging as this site is subject to frequent winter flooding.

Differences in frost sensitivity between green (i.e. subsp. *archeri*) and glaucous forms of *E. gunnii* have previously been reported (Lacaze 1962) and the present results are consistent with Barber's (1955) suggestion that the green or subglaucous forms are selected against in the more frost-prone habitats. However, the work of Harwood (1980) and Paton (1981) suggests that this may not be a direct result of variation in glaucousness *per se* as suggested by Thomas and Barber (1974a). The adaptive value of glaucous phenotypes in areas of high insolation is well recognized (e.g. Cameron 1970; Fung and Wright 1972; Thomas and Barber 1974a, 1974b) and reduced photosynthetic potential under low light intensities is the main reason suggested for selection against glaucous phenotypes in closed forest environments such as the subsp. *archeri* site at Projection Bluff (Cameron 1970; Thomas and Barber 1974b). However, from field observations it is difficult to identify the main selective factor favouring glaucousness *per se* since highly insolated and frost-prone habitats frequently coincide, as in the present study, and this combination clearly contributes to the harsh nature of the open woodland site (Shannon Lagoon) for seedling establishment.

Over the period studied, selection against the subsp. *gunnii* phenotypes in the subsp. *archeri* environment appears to be much less intense than against the subsp. *archeri* phenotype in the subsp. *gunnii* environments. Accordingly, the absence of at least seedlings which are similar to the '*divaricata*' phenotype at the subsp. *archeri* site could partly reflect restricted gene dispersal. However, altitudinally extreme morphs of subsp. *gunnii* are clearly also at a competitive disadvantage when grown at their opposite extreme. As also noted in several other species (e.g. *E. pauciflora*, Pyror 1959a; *E. vernicosa*, Jackson, unpublished data), the high altitude seedlings retain their slow growth rate at low altitudes and are thus unable to compete with faster growing, low altitude forms. In the present study, no clear data are available for the demise of the low altitude variant at the highest altitude site. However, Pryor (1959a) suggests that slow growth at higher altitudes may be advantageous in confining growth to a shorter, frost-free growing period, and several authors (e.g. Paton 1972; Marien 1979) allude to an association between growth rate and frost sensitivity. An increase in frost resistance with increasing altitude is commonly observed (e.g. Ashton 1958; Thomas and Barber 1974a; Marien 1979; Phillips and Reid 1980), although this relationship may be markedly displaced by other environmental considerations (present study; Paton 1972, 1981; Harwood 1980).

In the present trial the absence of marked differentiation in frost sensitivity of these subsp. *gunnii* populations (e.g. LH, SL, PF and SP; Figs 4 and 8) is notable as they encompass virtually the full altitudinal range of the complex (1150–600 m) and exhibit significant differences in growth rate. However, the specific sites occupied by subsp. *gunnii* at low altitudes are also subject to severe radiation frosts (e.g. Snug Plains; Davidson, unpublished data), which clearly suggests that the relatively high level of frost resistance maintained in low altitude populations is not a relic trait. This is consistent with the work of Harwood (1980) on *E. pauciflora*, where frost resistance may increase in low altitude sites subject to cold air drainage ('frost hollows'). In addition, preliminary data on *E. gunnii–archeri* (Potts, unpublished data) suggest that damage by low temperatures may be accentuated ($P < 0.05$) under waterlogged regimes. This is ecologically significant due to the trend for *E. gunnii–archeri* to occur on more waterlogged sites at lower altitudes. However, in view of the known complexity of the pre-conditioning process (e.g. Harwood 1980; Paton 1981), further work is clearly required on the genotype–site interaction for a full ecological interpretation of the low temperature response of this species.

Table 6. Psyllid (*Eucalyptel* sp.) infestation at the Projection Bluff (P2) garden over the 1980–81 season
The total abundance of psyllids per plant (summed over the period Nov.–Mar.), the percentage of plants infested, the heaviest infestation on any one plant and the mean (s.e.) abundance per plant at the time of maximum infestation (Jan. 1981) are indicated

Population	Total No./plant	Percentage of plants infested	Heaviest infestation	Mean abundance (s.e.) Jan. 1981
P1	1·8	42	8	1·2(0·38)
P2	4·6	100	11	3·5(0·90)
LH	25·6	100	54	22·7(4·19)
SL	10·2	100	26	7·1(2·45)
PF	9·7	100	30	10·5(2·57)
SP	7·8	75	14	7·7(2·66)

The significance of phytophagous insects as a major selective force in *Eucalyptus* ecology is well recognized (e.g. Burdon and Chilvers 1974*a*; Morrow 1977; Springett 1978), and is affirmed in this study where insect-grazing appeared to be a major factor limiting seedling growth at the higher altitude sites (e.g. Fig. 5). This contrasts with the observations of Burdon and Chilvers (1974*b*) on *E. pauciflora* where the amount of leaf-grazing by insects decreased with increasing altitude. There is evidence of host specificity at the subgeneric or specific level in *Eucalyptus* (see Pryor 1952; Burdon and Chilvers 1974*a*; Morrow 1977; Springett 1978) and the present study suggests that host preference may extend to the population level and be a significant factor in the competitive interaction between phenotypes within a single species. This is exemplified by differential grazing of seedlings from specific populations at both the Projection Bluff and Liawenee sites (Table 2; Fig. 5). At the Projection Bluff site in particular, intense preferential grazing of seedlings from the Shannon Lagoon population (Fig. 5) over several years, often extending to 90% defoliation, appears to be the main reason for the poor growth of this population at the subsp. *archeri* site (Figs 1–3).

In addition to preferential leaf grazing, there is limited evidence for population preference by some psyllid species. For instance, one species (*Eucalyptel* sp.) which occurred in large numbers at the Projection Bluff site in the 1980–81 season appeared to exhibit a preference for subsp. *gunnii* seedlings, particularly those from the Liawenee population (Table 6). In terms of coevolution of plant host and predator, it may be significant that the relative abundance of Homoptera insects is least at the Liawenee site (Table 4; Fig. 9). Differential predation may represent a simple primary effect (e.g. the presence or absence of secondary compound) or alternatively involve a complex variety of causes associated with the interac-

tion of several factors (e.g. plant form, drought, nutrition, etc.; see Springett 1978). Nevertheless, these results suggest that variation in the phytophagous insect fauna over the range of species may well be a significant factor in site adaptation and population differentiation.

In summary, this study indicates a degree of similarity in the selective response of populations from the same phenetic grouping (i.e. '*archeri*', '*divaricata*' and 'southern *gunnii*'; Potts and Reid 1985*a*) and, to some degree, the intensity of selection against a population in an alien habitat accords with the degree of genetic differentiation (as shown by Potts and Reid 1985*b*) from the local population. However, while variation in adult or seedling morphology may be associated with variation in fitness, there is no direct evidence as to whether the characters examined are adaptive *per se* or merely associated with other, perhaps physiological, characters more closely related to fitness. In addition, comparative estimates of fitness are based on the vegetative response and represent partial fitness values corresponding to a specific, relatively short phase in the life cycle of the species. Nevertheless, it is likely that, with time, increasing competition will accentuate the trends already evident.

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