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SIMILAR GEOGRAPHIC VARIATION AT THE *LAP* LOCUS IN THE MUSSELS *MYTILUS TROSSULUS* AND *M. EDULIS*

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Geographic variation in allele frequencies may result from direct selection of alleles at a locus; from indirect selection involving loci in gametic disequilibrium with the observed locus; or from random drift in isolated populations. Drift may be ruled out if repeated geographic patterns in allele frequency are associated with repeated environmental gradients (McDonald, 1987) or if differentiation occurs over distances that are small compared with the dispersal distance of the organism (Koehn et al., 1976). Distinguishing between direct selection and selection resulting from loci in gametic disequilibrium is difficult, but direct selection is the most likely explanation when two species that are polymorphic for the same alleles exhibit similar associations of allele frequency with the environment (Clarke, 1975). There are a number of examples of similar geographic patterns in pairs of species (Johnson, 1974; Harrison, 1977; Gill, 1981; Anderson and Oakeshott, 1984; Romano et al., 1987). These all consist of observations that allele frequencies in one species are correlated with frequencies in sympatric populations of a second species.

Here, we use a somewhat different approach, comparing patterns of allele frequencies in allopatric populations of the mussels *Mytilus trossulus* and *M. edulis*. The *Lap* locus has been extensively studied in *M. edulis* (Koehn and Hilbish, 1987), and the allozymes produced by the *Lap* locus in *M. trossulus* are electrophoretically indistinguishable from those of *M. edulis*. We report that, when estuarine and marine samples are compared, the Lap^{94} allele in *M. trossulus* is less common inside estuaries in Oregon, just as the Lap^{94} allele in *M. edulis* is less common inside estuaries in the northeastern United States. This is evidence that there is direct selection of alleles at the *Lap* locus.

MATERIALS AND METHODS

The locations sampled are shown in Figure 1. The Yaquina Bay samples (including site 2m, which was the closest marine sample to Yaquina Bay we could find) were collected in August 1984, and the remaining samples were collected in March 1987. For each of the four estuaries, one marine sample was collected outside the estuary. A single sample was collected inside three of the estuaries; five samples were collected inside Yaquina Bay, but they were pooled for the data analysis after being found not significantly heterogeneous (G test [Sokal and Rohlf, 1981 pp. 737–738], $G = 1.48$, $P = 0.83$). Electrophoretic methods are given in

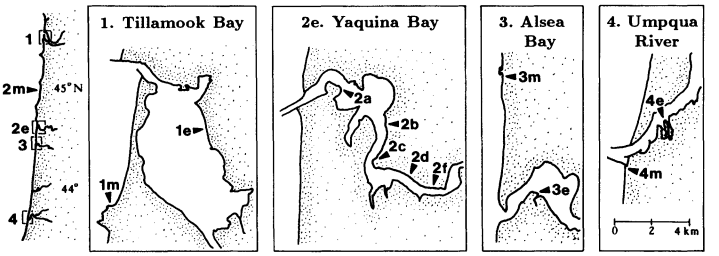

FIG. 1. Locations of *M. trossulus* samples. The map on the left shows the locations on the Oregon coast of the estuaries sampled. The four estuarine maps are drawn to the scale given on the Umpqua River map.

McDonald and Koehn (1988). Each individual was scored for the enzyme coded by the *Lap* locus, which was originally called leucine aminopeptidase but more recently has been designated aminopeptidase-I (E.C. 3.4.11.—; Young et al., 1979). In both 1984 and 1987, electrophoresis was performed on *M. trossulus* from Oregon alongside *M. edulis* from New York. Each LAP allozyme in *M. trossulus* was electrophoretically indistinguishable from an allozyme in *M. edulis*. The *Lap* alleles in *M. trossulus* were therefore given the same names as the alleles in *M. edulis*; this only implies the electrophoretic similarity of their allozyme products, not identity by descent. In *M. edulis* of the northeastern United States, alleles other than Lap^{94} maintain roughly constant proportions relative to each other; therefore, geographic variation has usually been summarized as variation in Lap^{94} frequency (e.g., Hilbish, 1985). The purpose of this study was to compare the pattern of geographic variation in *M. trossulus* with that in *M. edulis*, so alleles other than Lap^{94} were also pooled here.

Significance of the difference in allele frequency between estuarine and marine locations was tested using the Cochran-Mantel-Haenszel test (Snedecor and Cochran, 1980 pp. 210–213). Wright's inbreeding coefficient (F_{IS}) was calculated for each sample, with the expected number of heterozygotes corrected for small sample sizes (Levene, 1949) and all non-Lap^{94} alleles pooled. The mean F_{IS} was calculated using equation (6) of Kirby (1975), which corrects for differences in allele frequency among samples. Significance was tested using $F_{IS}{}^2N$, which is distributed as chi-square with one degree of freedom (Li and Horvitz, 1953). The mean F_{IS} was also calculated without pooling alleles using the method of Nei and Chesser (1983).

Because *M. galloprovincialis* is present in California (McDonald and Koehn, 1988), most individuals were also scored for peptidase-II (AAP; E.C. 3.4.11.—) and mannose-6-phosphate isomerase (MPI; E.C. 5.3.1.8), which would have revealed any *M. galloprovincialis* individuals or hybrids between *M. galloprovincialis* and *M. trossulus*. Only "pure" *M. trossulus* were found in Oregon.

RESULTS

At each of the four Oregon estuaries, the Lap^{94} allele in *M. trossulus* was less common inside the estuary than at the corresponding marine location (Table 1). The mean difference in Lap^{94} frequency between marine and estuarine sites was 0.07, which is significantly different from 0 ($Z = 2.29$, $P = 0.02$). Mussels have a planktonic larval stage lasting several weeks (Bayne, 1976), and entrainment of larvae is unlikely in the small, well-mixed estuaries of Oregon (Johnson and Gonor, 1982). Thus the differentiation in allele frequency found here on a scale of a few kilometers cannot be explained by random drift of isolated populations.

There was a deficit of heterozygotes at the *Lap* locus in *M. trossulus*. With all non-Lap^{94} alleles pooled, the mean F_{IS} was 0.165, which is significantly different from 0 ($F_{IS}{}^2N = 19.47$, $P < 0.001$). Without pooling alleles, the mean F_{IS} was 0.154; this value would be difficult to test statistically, since many genotypes have small expected numbers. Fourteen individuals had bands that were too faint or smeared to be scored for *Lap*, but even if all were heterozygotes, the heterozygote deficit would remain highly significant ($F_{IS}{}^2N = 14.84$, $P < 0.001$).

DISCUSSION

Estuarine samples of *M. edulis* in the northeastern United States also exhibit lower frequencies of Lap^{94}, when compared with marine locations, at Mill Creek and Scorton Creek, Massachusetts (Boyer, 1974; Koehn

TABLE 1. *Lap* allele frequencies in samples of *Mytilus trossulus* from Oregon. For each estuary, m indicates the marine sample, from outside the estuary, and e indicates the estuarine sample. The Yaquina Bay estuarine sample (2e) is the sum of the five samples from within Yaquina Bay; F_{IS} for this sample is the weighted mean of the individual F_{IS} values. The rare alleles Lap^{90} and Lap^{100} were pooled with Lap^{92} and Lap^{98}, respectively. All non-Lap^{94} alleles were pooled for calculation of Wright's inbreeding coefficient, F_{IS}. Asterisks indicate values of F_{IS} that are significantly different from 0 ($0.05 > P > 0.01$).

Sample	Lap^{92}	Lap^{94}	Lap^{96}	Lap^{98}	N	F_{IS}
1m	0.02	0.58	0.32	0.07	48	0.15
1e	0.08	0.47	0.35	0.10	73	0.15
2m	0.09	0.52	0.31	0.08	59	0.23
2e	0.08	0.46	0.37	0.09	279	0.15*
3m	0.10	0.51	0.31	0.09	72	0.09
3e	0.06	0.45	0.42	0.06	72	0.25*
4m	0.08	0.56	0.32	0.04	63	0.20
4e	0.12	0.50	0.29	0.08	48	0.18

et al., 1976) and at Lagoon Pond, Massachusetts; Peconic Bay, New York; and Long Island Sound (Koehn et al., 1976). (Other apparent examples of estuarine differentiation in "*M. edulis*" [Theisen, 1978; Gartner-Kepkay et al., 1983] now appear to result from inadvertent sampling of *M. trossulus* along with *M. edulis* [Koehn et al., 1984; Varvio et al., 1988].) Explaining the similar patterns in the two species without invoking direct selection of alleles at the *Lap* locus would require that the *Lap* locus be in gametic disequilibrium with a selected locus in both species. Additionally, in both species, Lap^{94} would have to be associated with an allele at the selected locus that was selected against inside estuaries. The simpler and more plausible explanation is that the selection involves the *Lap* locus itself.

Several possible selective factors differ between estuarine and marine habitats. Compared to marine environments, estuaries are likely to exhibit lower and more variable salinity, warmer summer temperatures, cooler winter temperatures, more variable temperatures, and perhaps differences in food quantity and type. In Long Island Sound, where Lap^{94} frequency differs by 0.43 between estuarine and marine populations, it has been suggested that selection results from a delicate interaction among timing of settlement, seasonal variation in food supply, temperature, and short-term variation in salinity (Hilbish and Koehn, 1985; Koehn and Hilbish, 1987). It seems unlikely that the particular combination of these factors present in Long Island Sound is repeated in each of the many estuaries where selection on *Lap* has been observed. Instead, it may be that a simpler selective factor that is generally associated with estuaries is sufficient to produce some selection of alleles of the *Lap* locus, while the conditions at Long Island Sound interact to produce the especially dramatic selection seen there.

Wahlund effects are not a plausible explanation for the heterozygote deficit in *M. trossulus*. The mean F_{IS} of 0.165 would require a variance in allele frequency of the source populations of 0.04, corresponding to mixing of two populations differing in allele frequency by 0.40. The observed variance in Lap^{94} frequency is 0.002, far too small to explain the observed deficit.

Heterozygote deficits are a common observation in marine bivalves, one for which no satisfactory explanation is apparent (Singh and Green, 1984; Zouros and Foltz, 1984). Repeated differences in *Lap* allele frequency associated with estuaries occur in the bivalve *Geukensia demissa* (Garthwaite, 1986), in addition to *M. trossulus* and *M. edulis*. There may be a relationship between the selection that produces estuarine differentiation and the process that produces heterozygote deficits, but the nature of any such relationship remains to be discovered.

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ACACIA MANGIUM: A TROPICAL FOREST TREE OF THE COASTAL LOWLANDS WITH LOW GENETIC DIVERSITY

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There are more than 1,000 described species of *Acacia*, of which about 650 occur in Australia, the rest occurring largely in Africa and tropical America (Boland et al., 1984). Only nine of the Australian species in this genus extend northward into either Papua New Guinea or Indonesia (Skelton, 1987). One of these, *A. mangium* Willd., has emerged in the last decade as a major forest plantation species for tropical moist environments, (National Academy of Sciences, 1983; Turnbull, 1986) particularly in Sabah, Malaysia, on degraded soils colonized by *Imperata cylindrica* L. Partly for this reason, we undertook a study of the genetic diversity in natural populations of *A. mangium*. As a result we are able to report the first study of the distribution of genetic variability of any plant species co-occurring in the South-East Asian and Australian floras. Also preliminary estimates of genetic diversity are presented for eight other species of *Acacia*.

The last land bridges to the Australian mainland were with Tasmania and New Guinea. The Torres Strait between Australia and New Guinea was last formed less than 10,000 years ago (Walker, 1972; Galloway and Kemp, 1980). It apparently first came into existence some time in the Pleistocene (Doutch, 1972), but the land bridge has come and gone several times subsequently as a result of retreating sea levels during periods of glaciation. Originally, the Torres Strait was considered a major floristic demarcation zone between the Malesian and Australian floras, but currently it is thought of more as an ecological boundary than as a geographical one (Barlow, 1981). It might be predicted that species now occurring in the plant communities occupying the coastal lowlands around the strait would have recolonized these areas from small scattered refuges where they survived during the interglacial periods of high sea levels.

MATERIALS AND METHODS

Acacia mangium occurs in northern Queensland, the Western Province of Papua New Guinea, and the Indonesian provinces of Irian Jaya and Maluku (Fig. 1; Doran and Skelton, 1982; National Academy of Sciences, 1983; Turnbull, 1986). Over this geographic range, *A. mangium* grows primarily in coastal tropical lowlands on margins of closed forest, and in open forest and woodland. The species appears to be a strong colonizer of areas disturbed either by fire or man (Turnbull, 1986; Skelton, 1987).

Seed collections (Fig. 1, Table 1) were made by the CSIRO Tree Seed Centre (Doran and Skelton, 1982; Turnbull et al., 1983). For each population, seeds were collected from 5–30 field trees. Where possible the number of seedlings assayed per population (see Table 1) was divided equally between the number of parental trees sampled.

Starch-gel electrophoresis was used to determine allozyme genotypes in germinating open-pollinated seed. Each seedling was assayed for 18 enzyme systems and scored for electrophoretic variants at 30 loci. Details of enzyme systems, electrophoretic procedures, and enzyme stains are given in Moran et al. (1989). To get estimates of genetic variability for other acacias a small number of plants were assayed isozymically from one population for each of eight species. For each of these