Ecology, 65(4), 1984, pp. 1038–1051

DISPERSAL ADAPTATIONS OF SOME *ACACIA* SPECIES IN THE AUSTRALIAN ARID ZONE[1]

D. W. Davidson
Department of Biology, University of Utah, Salt Lake City, Utah 84112 USA

AND

S. R. Morton[2]
School of Biological Sciences, University of Sydney, New South Wales 2006 Australia

Abstract. Most Australian representatives of the genus *Acacia* have diaspores with arillate appendages indicative of adaptation for active dispersal by animals. Based on physical and chemical characteristics of these arils and mechanisms of diaspore presentation, a number of arid zone acacias can be distinguished as probable ornithochores, myrmecochores, or species lacking active dispersal by animals. Two factors suggest that dispersal adaptations are evolutionarily labile in the face of changing selection pressures. Both myrmecochores and ornithochores are prevalent in each of the three largest taxonomic sections of the Australian subgenus *Phyllodineae.* Second, diaspores of at least one species, *Acacia ligulata,* exhibit geographic variation, resembling those of myrmecochores in one population and ornithochores in a second population.

The colorful lipid-rich arils of avian-dispersed species are nutritionally more valuable than the relatively small, white appendages of ant-dispersed species with similar-sized propagules. While ants often collect the diaspores of ornithochorous acacias, we have no evidence that birds use the arils of myrmecochores. Patterns of seedling establishment on ant mounds, and under the canopies of trees where birds perch and defecate, are consistent with these observations. Exploitation of diaspores by birds may help to reduce the destruction of seeds by parasitoids and, in part, compensate for the higher aril expenditures (per milligram of propagule) in avian-dispersed species.

Dispersal of seeds by both ants and birds directs seeds to microhabitats where nutrients are concentrated and water resources are more plentiful and/or are used more efficiently. Similarities between mound and subcanopy microhabitats may have facilitated evolutionary transitions between myrmecochory and ornithochory. The nutrient poverty that generally characterizes Australian soils has possibly played a role in selecting for seed dispersal by ants and birds in this genus as well as in many other Australian plants.

Key words: Acacia; *Australian arid zone; dispersal ecology; fruit quality; myrmecochory; ornithochory; seed parasitoids; soil nutrients.*

INTRODUCTION

Of the estimated 1100–1200 species of *Acacia* worldwide (Ross 1981), ≈66% comprise the Australian subgenus *Phyllodineae* (syn. *Heterophyllum*) (Maslin and Pedley 1982). Members of this largely endemic taxon show distinctive adaptations for seed dispersal. In Africa and the Americas, the seeds of many acacias are adapted for dispersal by water and wind (Lamprey et al. 1974), while other species have seeds disseminated by ruminant ungulates that eat the leathery, nutritive pods (Lamprey 1967, Janzen 1969, Janzen and Martin 1982). Australia has no native ruminants, and here the *Acacia* diaspores have arillate appendages that suggest active dispersal by other groups of animals. (Throughout this paper, we will use the term "aril" to describe both true arils and funicular appendages that function as arils; see Vassal [1971] and Pijl [1982] for the distinction.) Among others of the world's acacias, those most similar to Australian forms in dispersal ecology are probably the polyphyletic neotropical swollen-thorn species, whose seeds are embedded in fleshy pulp and probably dispersed by birds and bats (Janzen 1969).

In attempting to identify likely dispersal agents, we have investigated adaptations of 20 *Acacia* species inhabiting arid inland Australia. Based on differences in the physical and chemical characteristics of arils and in the means by which diaspores are presented or displayed, we separate species into three distinct dispersal categories, and assess the degree to which this separation is consistent with available evidence on animals known to transport diaspores. Finally, we investigate potential ecological, phylogenetic, and biogeographic correlates of dispersal adaptations in the Australian acacias.

METHODS

Identification of dispersal syndromes

Our studies took place during spring (September–November) of 1979, 1980, and 1981 at the locations described in Table 1, and included all species of *Acacia*

---

[1] Manuscript received 21 October 1982; revised 30 June 1983; accepted 5 July 1983.

[2] Present address: Alligator Rivers Region Research Institute, Office of the Supervising Scientist, Jabiru, Northern Territory 5796 Australia.

TABLE 1. Description of collecting localities and diaspore characteristics of *Acacia* species from arid Australia. ND = no data.

						Seeds parasitized	
Acacia species* (section)	Locality	Date	AC†	OSP‡	Dispersal agents§	*N* (no. seeds)	% para-sitized
1) *tetragonophylla* (Ph)	141.5°E, 29°S	Oct 80	Y	L	Ant (*R, Rm, M*)	37	5
	120°E, 22.5°S	Sep 81			Bird (*L, Ar*)	1861	1
2) *coriacea* (Pl)	133°E, 22.5°S	Oct 81	Y	L	ND	621	8
3) *cowleana* (J)	131°E, 17°S	Sep 81	Y	L	Ant (*R*‖)	521	4
4) *holosericea* (J)	133.5°E, 17.5°S	Oct 81	Y	L	Ant (*P*)	907	0
5) *tenuissima* (J)	131°E, 17°S	Sep 81	O	L	Ant (*R*‖,*C*)	70	3
6) *ligulata* (Ph) (Population 1)	141.5°E, 29°S	Nov 81	Y	L	Ant (*I, P*)	274	2
7) *ligulata* (Ph) (Population 1)	141.5°E, 29°S	Nov 81	R	L	Ant (*I, P*) Bird (*L, Ar*)	481	3
8) *ligulata* (Ph) (Population 2)	132.5°E, 22°S	Oct 81	O	L	ND	752	22
9) *acradenia* (J)	127°E, 17.5°S	Sep 81	W	O	Ant (*R*)	1976	1
10) *ancistrocarpa* (J)	119°E, 20°S	Sep 81	W	O	Ant (*R*‖)	1091	9
11) *eriopoda* (J)	126°E, 17.5°S	Sep 81	W	L	Ant (*P*)	1317	12
12) *lysiphloia* (J)	131°E, 17°S	Sep 81	W	O	Ant (*R*)	273	24
13) *tumida* (J)	126°E, 17.5°S	Sep 81	W	O	ND	1286	11
14) *dichtyophleba* (Ph)	133.5°E, 22°S	Oct 81	W	T	ND	1557	17
15) *ramulosa* (J)	121.5°E, 28°S	Sep 81	W	L	ND	199	19
	135°E, 27°S	Oct 81				765	15
16} *pruinocarpa* (Ph)	120°E, 27°S	Sep 81	W	T-O	ND	654	2
17) *aneura* (J)	141°E, 31°S	Oct 80	W	O	Ant (*M, P*)	131	56
	120°E, 22.5°S	Sep 81				407	33
18) *victoriae* (Ph)	141°E, 31°S	Nov 81	W	T	Ant (*R, Rm, I*)	222	34
19) *cana* (Pl)	141.5°E, 29°S	Oct 80	W	L	Ant (*R, Rm, M*)	49¶	45
20) *adoxa* (L)	131°E, 17°S	Sep 81	W	T-O	ND	ND	

* Species determinations by B. Maslin, except for nos. 6, 7, and 19 (identified by L. Pedley) and 18 (identified by S. Jacobs). Sections within the subgenus *Phyllodineae*: J = *Juliflorae*, Pl = *Plurinerves*, Ph = *Phyllodineae*, L = *Lycopodiifoliae*.

† AC = aril color: Y = bright yellow, O = orange, R = red, W = white (includes pale yellowish-white and "dirty" [brownish] white).

‡ OSP = orientation of seeds in pods: L = longitudinal; O = oblique; T = transverse.

§ Ants: R = *Rhytidoponera mayri* spp. group; Rm = *Rhytidoponera metallica* spp. group; I = *Iridomyrmex purpureus* spp. group; M = *Melophorus*; P = *Pheidole*. Birds for which observations of both foraging and fecal samples of Forde (*in press a*) document use of *Acacia* arils: L = *Lichenostomus virescens*; Ar = *Acanthagenys rufogularis*.

‖ Data only from experimental trials in which diaspores were presented in bait trays to ant colonies.

¶ Seeds collected from refuse heaps on ant mounds rather than from tree or shrub.

that we encountered in fruit. For each species population, we noted aril color, morphology of seed pods, orientation of seeds in legumes, mode of diaspore presentation or display at maturity, and, whenever possible, animals transporting diaspores and eating arils. We collected approximately the same number of seed pods from each of a number of individual plants in each species population and examined the seeds for evidence of destruction by parasitoids. Seeds were scored as infested if they contained exit holes or developing larvae or if they were aborted at early stages of development with visual evidence of parasitoid presence. In general, seeds with developing larvae could be distinguished by their lighter color and very thin seed coats that caused them to crack readily under pressure. However, over a period of ≈1 mo, a very few previously undetected parasitoids emerged from seeds stored in plastic vials. Rates of seed infestation reflect these late emergences. Spot checks of seeds germinated after scarification and soaking in distilled water failed to reveal any additional instances of seed parasitism.

In the laboratory, we analyzed the physical and chemical properties of diaspores with intact (uninfested) seeds. With a Sartorius analytical balance, we determined wet and dry masses of individual seeds and their arils. Arils from many different seeds of each species population were combined for analysis of their percent dry mass content of lipid (by Soxhlet extraction), total nonstructural carbohydrate (modified Weinmann method, Smith 1969) and total Kjeldahl nitrogen (digestion in Tecan Block Digestor, colorimetric analysis of total organic nitrogen with Technicon Auto Analyzer). Using the standard conversion factor of 100 mg of protein per 16 mg total nitrogen, we calculated protein content as a percentage of dry

TABLE 2. A summary of the investigations of small shrub (SS) association in Sturt National Park. Small shrub densities on mounds or beneath trees were compared pairwise to densities in quadrats nearby.

	SS establishment studied in relation to:	
Locality	*Rhytidoponera* mounds	Subcanopies*
	Small shrubs censused	
Olive Downs Homestead		
Downs South and Downs Park	*A. tetragonophylla* *A. aneura*	*A. tetragonophylla*
Stony Downs	*A. tetragonophylla*	trees absent
30 km east of Fort Grey Homestead		
Camp David I	mounds absent	*A. tetragonophylla* *A. aneura*
Camp David II	mounds absent	*A. ligulata* (Pl)

* Pattern of establishment in relationship to *A. aneura* canopies except at Camp David I, where SS's were enumerated beneath the canopies of both *A. aneura* and *Atalaya hemiglauca* (10 trees each) and Camp David II, where very low densities of *A. aneura* led us to use *Atalaya hemigaluca* exclusively.

mass. For *A. cana*, we had sufficient aril material to complete only the analyses of nitrogen (protein) and lipid, and thus have no estimate of carbohydrate content or of total energy. Fruits of *A. adoxa* could not be collected in sufficient quantity for analyses of physical or chemical properties or rates of infestation by parasitoids, but we do have observations of aril color and diaspore presentation.

A comment is in order here on our classification of acacias 6 through 8 in Table 1. Although the three variants have been included under *A. ligulata* (B. Maslin and L. Pedley, *personal communication*), we differentiate them here because of their distinctive diaspore characteristics. While variant 8, growing near Barrow Creek, Northern Territory, has orange-arillate seeds, variants 6 and 7, co-occur at our study site in Sturt National Park, New South Wales, and have diaspores with yellow and red arils, respectively. It is not unusual to find two such color morphs growing in a single *Acacia* population; this occurs in *A. cyclops*, *A. rostellifera* (a very close relative of *A. ligulata*), and probably in other species as well (B. Maslin, *personal communication*). We will consider forms 6 and 7 to be morphological variants within the same species population (P1). Variant 8, or population 2 (P2) of *A. ligulata* is sufficiently distinctive in characteristics related to seed dispersal that we will treat it independently of population 1 in many of our analyses.

Patterns of seedling establishment

Seedling establishment is apparently a rare event in many species of *Acacia*, and only in Sturt National Park, protected from grazing by domestic and feral stock since 1975, did we observe significant recruitment of young plants. Here, we were able to quantify the spatial pattern of plant establishment for *A. ligulata* (P1), *A. tetragonophylla*, and *A. aneura*. While *A. ligulata* is a true shrub, individuals of *A. tetragonophylla* (occasionally) and *A. aneura* (often) grow into large, single-trunked trees. Small individuals of all three species can be reproductive, and we cannot accurately refer to them as seedlings or saplings. We therefore designate them here as small shrubs (SS). Preliminary observations had suggested that ants and birds might be the principal animals involved in dispersal. For this reason, we compared the SS densities on ant mounds or beneath trees (where perching birds may defecate seeds) with those in paired random plots off mounds or distant from canopies. Table 2 identifies the sites at which one or both of these comparisons were carried out and the comparisons that were possible at each site.

The ant mounds censused are those of an omnivorous species in the *Rhytidoponera mayri* species group (species B among S. R. Morton's specimens in the Australian National Insect Collection, Canberra). Colonies of these ants construct nest mounds that are often 30 cm or more in height and appear to persist for many years (Davidson and Morton 1981*a*). At three sites (Table 2), we recorded SS densities of *A. tetragonophylla* and *A. aneura* on each *Rhytidoponera* mound observed in a directional transect through the site. A 0.25-m^2 square sampling frame was centered over the entrance hole on the mound and arranged to include the maximum number of *Acacia* individuals. Densities in these quadrats were compared with paired samples taken by tossing the frame to a random position off the mound and again rotating it about its center to include the maximum number of acacias. Maximization of *Acacia* numbers introduced no risk of species bias, because we never encountered more than one *Acacia* species per mound.

Associations of *Acacia* SS's with tree canopies were measured by sampling circular areas of equal radii centered directly beneath the canopy or well outside the canopy, 9 m from the tree. The radius was chosen to be 3.5 m, or ≈0.3 m greater than the average measured radius of tree canopies ($N = 80$; SD ≈ 1.0). Thus, the minimum distance between the canopy border and the edge of the open sample averaged 2.0 m. For consecutive trees, samples positioned in the open were taken alternately to the north, south, east, and west of the trees. If another large tree was present in the direction first specified, the direction next in order was chosen. Trees were used as encountered on directional transects through the study sites.

Several practical problems prevented us from taking our measurements within the framework of a completely balanced design at each site. At the Downs South and Downs Park localities, *A. aneura* was the only common canopy species. Thus, we could not distinguish which of the often numerous subcanopy seedlings may have originated from avian-dispersed seeds and which were from seeds that fell from the parent plant to the ground below. *Acacia aneura* was rare at Camp David site II, and only at Camp David site I were we able to study the distribution of this species with respect to a different canopy tree, *Atalaya hemiglauca*. A more complete sampling design would also have included censuses of acacias on *Rhytidoponera* mounds located both beneath canopy trees and in open microhabitats. However, subcanopy microhabitat comprised a very small proportion of the total area, and although it was possible to find an occasional *Rhytidoponera* mound in the subcanopy, these were rare occurrences, and we limited our sample to mounds located away from the influence of canopy trees.

Finally, in November of 1981, we returned to Olive Downs Park to assess the relative sizes and fruiting conditions of *A. tetragonophylla* plants in subcanopy and open microhabitats. The sampling procedure was identical to that used previously except that instead of merely quantifying SS densities, we scored individuals as to reproductive condition (fruiting or nonfruiting) and measured them to the nearest 5 cm in length (broadest dimension), width (narrowest dimension), and maximum height. Sizes of individual plants were estimated by the products of their length, width, and height and used to estimate the proportion of total plant biomass in a given area that consisted of plants that were in fruit. To boost sample sizes for plants in the open, three open quadrats were sampled for each quadrat censused in the subcanopy.

Soil nutrient analysis

Because plant biomass appeared to be greater and reproduction more prolific beneath tree canopies than in surrounding habitats, we hypothesized that potentially limiting plant nutrients might be concentrated in these microhabitats. In November of 1981, soil samples were collected from matched quadrats positioned at random in subcanopy and open microhabitats. After removal of surface litter, a square soil sampling device (10 cm on a side) was driven into the ground to a depth of 5 cm. The resulting 500 cm^3 volume of dry (sun-baked) soil was removed to a paper bag and transported to the Commonwealth Scientific and Industrial Research Organization Soils Laboratory in Glen Osmond, South Australia, within 2 d for drying and storage prior to analyses. Samples from subcanopy and open microhabitats were taken in relationship to the canopies of 15 different trees (all *A. aneura*) and analyzed for pH, electrical conductivity, and various chemical constituents (see below). A random subsample of soils from each microhabitat type was also analyzed for exchangeable cations and particle size. Analytical procedures were identical to those used in earlier investigations of nutrient concentration on ant mounds (Davidson and Morton 1981*a*). To test for differences in soil properties of subcanopy and open microhabitats, we used *t* tests when the assumptions of this parametric procedure were met, and otherwise used the nonparametric sign test to compare paired samples taken in the vicinity of the same nurse trees.

RESULTS

Identification of dispersal syndromes

Based on aril color, legume morphology, and seed orientation in pods, the majority of *Acacia* species studied tend to separate into two major groups. Diaspores of acacias 1 through 8 in Table 1 have colorful arils (red, bright yellow, or orange), are oriented longitudinally in valves of the legumes, and are retained and displayed in the legumes on the shrub or tree. Diaspores of the remaining 14 species in Table 1 have white or off-white arils and are oriented longitudinally, obliquely, or transversely in the legume. The majority of these species do not retain and display diaspores on the plant.

Acacias 1 through 8 in Table 1 exhibit a heterogeneous assortment of adaptations for displaying brightly colored diaspores on the plant (Fig. 1). At maturation, pods of *A. coriacea* spiral along their longitudinal axes to reveal brightly colored arils on seeds retained between open valves of the legume (Fig. 1a). A much looser but otherwise similar spiralling occurs in the legumes of *A. cowleana*. In comparison, legumes of *A. holosericea*, a close relative of *A. cowleana*, do not spiral but are tightly coiled (Fig. 1b), and retain the majority of their diaspores with yellow arils visible through partially dehisced pods. In *Acacia tenuissima*, a more distant relative of *A. cowleana* and *A. holosericea* (B. Maslin, *personal communication*), some diaspores are supported from below on the curved valves of open legumes, while others dangle by their arils (Fig. 1c). All three species, *A. cowleana, A. holosericea*, and *A. tenuissima*, have legumes clustered on receptacles, where they remain firmly attached even after most or all of their diaspore contents have vanished. The coiled legumes of *A. tetragonophylla* fold open, and the separated valves serve as shelves on which seeds, completely encircled by bright yellow arils, are displayed (Fig. 1d). Unlike the legumes of other species in this group, those of *A. ligulata* (all three variants) are linear. However, as they are held in a semierect position, valves curling open from their distal ends again provide platforms for display of diaspores (Fig. 1e).

The 12 acacias with white arils also form a heterogeneous assemblage with respect to pod morphology and diaspore presentation (Fig. 2). However, most of these species appear to lack any particular mechanism for displaying diaspores on the plant, and some species actually present diaspores at ground level. Legumes of *A. lysiphloia* hang vertically from the plant and open from their distal ends to drop diaspores on the ground

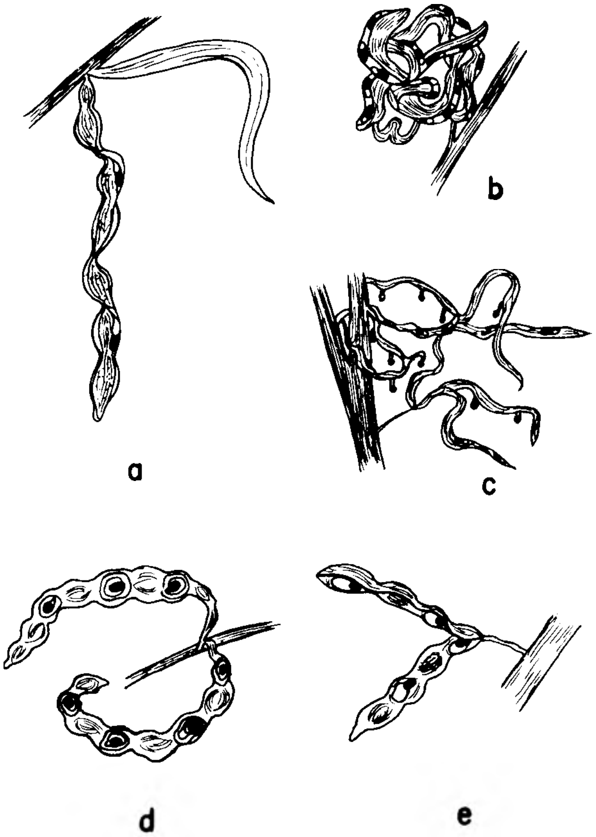

FIG. 1. Presentation of diaspores in acacias with colored arils: a *A. coriacea*; b *A. holosericea*; c *A. tenuissima*; d *A. tetragonophylla*; e *A. ligulata*.

below. In *A. adoxa*, diaspores are shed in a similar fashion, but from pods held horizontally and splitting along their lower sutures (Fig. 2a). In *A. tumida*, legumes are held in a semierect posture and valves uncurl from one another, beginning at their distal ends. Since a plane formed by joining the sutures of the pod would be perpendicular to the ground surface, diaspores fall readily from valves as they separate. *Acacia* species *aneura* (Fig. 2b), *victoriae*, *dictyophleba*, and *pruinocarpa* have linear to oblong, papery legumes that often are shed unopened or opened with seeds still attached. *Acacia ramulosa* drops its massive legumes (Fig. 2c) directly beneath the shrub, where we found them in abundance and unopened months after the fruiting season had concluded. Both *A. ancistrocarpa* and *A. acradenia* appear to show intermediate modes of diaspore presentation, shedding some diaspores on the ground, while retaining others. Legumes of *A. ancistrocarpa* (Fig. 2d) are held in a semierect posture and spring open explosively to shed their diaspores. A few diaspores remain in separated valves on the shrub and are displayed in a manner not unlike those of *A. ligulata*. The pods of *A. acradenia* (Fig. 2e) hang vertically from the plant and open from their proximal ends. Once the connection between valves is broken at the proximal end, one valve falls (often within seconds) to the ground with its seed contents. Half of the diaspores remain appended on small white arils from the valve still attached to the plant. Finally, *A. eriopoda* represents an exception to the above pattern of display for white-arillate species. The linear pods of this species (Fig. 2f) hang vertically from the plant and open at their distal ends. Although a few diaspores may fall as valves separate, many remain to dangle loosely by their arils.

Our analyses of the physical and chemical properties of arils and diaspores are reported in Table 3. For a given dispersal agent, the profit/cost ratio associated with handling and consumption of diaspores should vary in proportion to E/WMD. Here, E is the average energy per individual aril, and WMD is the mean wet mass of diaspores. If the ratio of E/WMD is plotted against percent water content, another potential component of profit, a relatively distinct separation of species results (Fig. 3). The separation of species shown in Fig. 3 has several interesting features which differentiate it from our initial species classification based simply on aril color and diaspore presentation. (1) By virtue of its very small E/WMD ratio and relatively

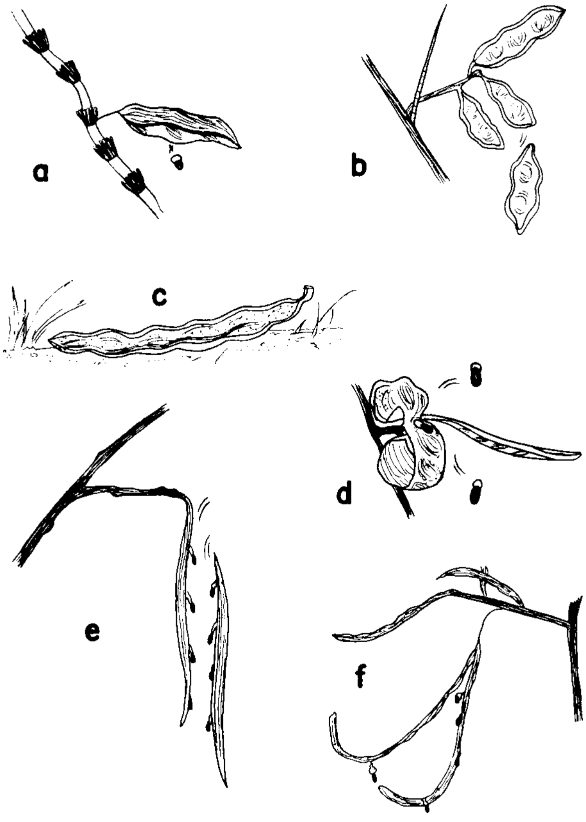

FIG. 2. Presentation of diaspores in white-arilled acacias: a *A. adoxa*; b *A. aneura*; c *A. ramulosa*; d *A. ancistrocarpa*; e *A. acradenia*; f *A. eriopoda*.

TABLE 3. Physical and chemical properties of arils and diaspores of *Acacia* species. Species numbers refer to the list in Table 1. Diaspore = seed + aril. Relative dry mass of aril = (dry mass of aril)/(wet mass of diaspore). Aril composition values are means of two determinations. CHO = nonstructural carbohydrate. E/WMD = (energy content per aril)/(wet mass of diaspore). Energy values were calculated with the conversion factors of Brody (1945) for lipids (39.50 kJ/g) and carbohydrates (17.31 kJ/g) and Ricklefs (1974) for useable protein (17.97 kJ/g); these conversion values were originally reported in calories per gram. ND = no data.

Species no.	Wet mass of diaspore (mg)	Dry mass of aril (mg)	Relative dry mass of aril	Aril water content (% of wet mass)	Aril composition (% of dry mass)			E/WMD (J/mg)
					Lipid	CHO	Protein	
1	13.8	3.6	0.26	7.1	57.5	10.2	17.8	7.15
2	119.1	17.4	0.15	18.3	56.2	19.8	23.0	4.31
3	15.4	1.6	0.10	20.5	52.8	16.4	25.2	2.97
4	11.5	0.7	0.06	22.2	53.4	14.1	26.5	1.71
5	6.6	1.1	0.17	10.6	63.2	14.5	18.9	5.10
6	45.7	10.9	0.24	5.5	54.3	10.1	16.9	6.23
7	61.3	16.4	0.27	6.2	49.5	8.9	21.9	6.65
8	50.6	3.9	0.08	9.4	52.8	12.7	33.1	2.22
9	10.1	0.8	0.08	9.8	36.3	10.5	24.3	1.67
10	61.4	3.9	0.06	5.4	24.6	12.7	23.2	1.00
11	17.2	0.8	0.05	6.9	19.9	20.4	31.6	0.79
12	22.0	1.2	0.05	7.8	34.9	20.6	27.1	1.21
13	60.3	3.8	0.06	6.7	38.8	13.9	28.8	1.42
14	9.4	0.3	0.03	8.1	17.6	20.7	26.5	0.54
15	100.8	0.6	0.01	13.8	67.9	19.1	8.7	0.17
16	29.2	1.4	0.05	6.8	9.1	42.4	10.1	0.59
17	7.4	0.2	0.03	4.8	18.3	32.4	23.9	0.46
18	29.2	0.6	0.02	6.7	2.9	48.2	9.0	0.21
19	32.2	0.5	0.02	26.4	49.0	ND	13.3	ND

high aril water content, *A. ramulosa* (species 15) falls out as distinctive from the two major species groups. (2) The two populations of *A. ligulata* studied (6 and 7 vs. 8 in Table 1) clearly separate into alternate groups. The orange-arillate variant collected near Barrow Creek, Northern Territory, provisions diaspores with a markedly lower ratio of E/WMD than do the yellow and red-arillate plants from Sturt National Park, New South Wales. (3) Among the species in Group II of Fig. 3, there is a significant inverse relationship between percent water content of arils and E/WMD ($r = 0.95$, $P < .01$; values averaged for the two variants of *A. ligulata* [P1]). On the other hand, percent water content is positively correlated with E/WMD in Group I species ($r = 0.66$, $P < .05$). Both of these correlations are independent of the minor contribution of aril water to WMD ($\bar{x} = 0.4\%$, SD = 0.3% in Group I species, and $\bar{x} = 2.2\%$, SD = 0.7% in Group II species [Fig. 3]). (4) Finally, the four species with flat papery legumes (species 14, 16, 17, and 18, circumscribed by the dotted line) cluster in Fig. 3 with relatively low values of E/WMD, although they are not sharply demarcated from other species in Group I.

The ratio of E/WMD is greater for species in Group II than for those in Group I (Mann-Whitney U test: $U_{s[6,10]} = 1$, two-tailed, $P < .002$; data averaged for two variants of *A. ligulata* P1). Two major factors contribute to this difference. Aril size generally increases with seed size, but dry mass of aril per unit wet mass of diaspore is greater among species in Group II $U_s = 0.5$, $P \ll .002$). For this same set of species, arils have a greater lipid content as a percentage of their dry mass ($U_s = 0$, $P < .001$), and lipid furnishes more than twice as many joules per gram as either carbohydrate or protein. Proportionate dry mass investments in total nonstructural carbohydrate (TNC) and protein do not differ significantly between arils of the two groups of species, though arils of Group I species tend to be slightly richer in protein. *Acacia pruinocarpa* and *A. victoriae* are distinctive in having arils with exceptionally high TNC content and relatively low levels of protein. If these two members of section *Phyllodineae* are omitted, Group I arils have proportionately greater protein content than those in Group II ($U_{s[6,8]} = 6.5$, $P < .026$), but the classes still do not differ in percentage TNC.

Table 1 gives the identities of ants and birds that are potential agents of seed dispersal. (Note that data on birds are not our own.) While the relatively energy-rich arils of Group II species are eaten by both ants and birds, based on available evidence, those of Group I species are used exclusively by ants. We considered ants to be potential agents of dispersal if they transported arillate diaspores and deposited visibly undamaged *Acacia* seeds in their refuse heaps with arils removed. Also distinguished in this table are *Acacia* species whose diaspores were collected by *Rhytidoponera* (*mayri* species complex) from bait trays presented to colonies near Cunyu, Western Australia, and Fowlers Gap, New South Wales.

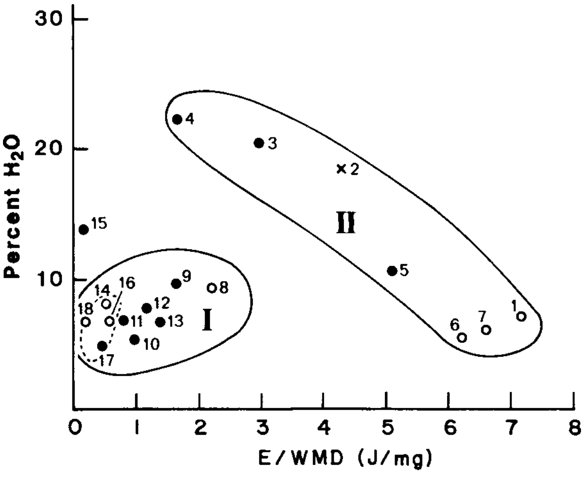

FIG. 3. Percent water content of aril vs. the mean energy reward (J) per mean wet mass of diaspore (mg). Separation of species is discussed in the text. Sections of the subgenus *Phyllodineae*: ○ *Phyllodineae*; • *Juliflorae*; × *Plurinerves*.

TABLE 4. Comparisons of *Acacia* small shrub densities under tree canopies and in the open nearby (Camp David sites I and II).

		Plant densities (number per 38.5 m^2) under:			
		Acacia aneura		*Atalaya hemiglauca*	
Species	Site	Canopy	Open	Canopy	Open
		Mean ± standard deviation			
A. aneura	I	0.70 ± 1.06	0.80 ± 1.14	0.30 ± 0.67	0.10 ± 0.32
A. tetragonophylla	I	1.00 ± 1.15	0.20 ± 0.42*	4.00 ± 4.45	0.80 ± 2.20*
A. ligulata (P1)	II	0.80 ± 1.20	0.20 ± 0.31**	...	...

* Comparisons between canopy and open samples are significant at $P < .05$ ($t_{[18]} = 2.06$ for *A. aneura* canopy, and $t_{[18]} = 3.51$ for *A. hemiglauca* canopy).

** $P < .01$ ($t_{[38]} = 2.52$). Tests are one-tailed for *A. tetragonophylla* and *A. ligulata*, posited ornithochores, and two-tailed for *A. aneura*, an hypothesized myrmecochore.

Most ants of the Australian arid zone cannot be identified confidently to species, but we give species groups where these are known. Approximate body lengths of ants (measured with binocular microscope and ocular micrometer) were determined for representative ants in each genus or species complex. In order of decreasing body size, these taxa are *Rhytidoponera* (*mayri* species complex, 12 mm), *Iridomyrmex* (*purpureus* complex, 9 mm), *Rhytidoponera* (*metallica* species complex, 7 mm), all predominantly predatory ants, and the largely granivorous or omnivorous genera, *Melophorus* (size-polymorphic at 3–5 mm) and *Pheidole* (3 mm). Although *Acacia* seeds surrounding the nest entrances of granivores sometimes appeared to be damaged, at least some of the seeds had escaped any visible damage.

Seed parasitoids

In general, rates of infestation by seed parasitoids tended to be lower in species or variants with colored arils (species numbers 1–8, Table 1) than in those with white or off-white arils (numbers 9–19; $U_{s[7,11]} = 16.5$, $P \approx .05$ in two-tailed test). Yellow- and red-arillate variants of *A. ligulata* (P1) were treated as a single population, with their parasitization percentage computed as an average weighted by sample size. For each of three species for which we have replicate samples from geographically distinct populations, we used the parasitization percentage associated with the largest sample size. In two of three cases, this procedure biased us against the result we report.

Among species with colored arils, *A. ligulata* (P2) has an exceptionally high rate of seed parasitism. The clustering of this species with white-arillate acacias in Fig. 3 helps to produce an even more pronounced difference in rates of seed parasitism between Groups I and II ($U_{s[6,12]} = 9.5$, $P \approx .025$). No relationship is apparent between percentage parasitized and either taxonomic (sectional) affiliation or seed size ($P \gg .05$ for pairwise comparisons in Mann-Whitney *U* test and Spearman Rank Correlation, respectively).

While we did not attempt to identify all the parasites encountered in our studies, those that emerged as adults were identified as chalcid wasps (Hymenoptera, Chalcidae).

Small shrub establishment

Patterns of SS establishment should permit us to test for the importance of ants and birds in the dispersal of individual species of *Acacia*. At Camp David site I, SS's of *Acacia aneura* showed no significant association with tree canopies (Table 4). SS's were no more concentrated under *A. aneura* canopies ($t_{[18]} = 0.27$) or *Atalaya* canopies ($t_{[18]} = 1.13$) than in open plots in the vicinity of each of the respective tree species. As expected, however, seedlings of *A. aneura* occurred at greater densities in open samples near *A. aneura* trees than in open samples near *Atalaya* canopies (one-tailed $t_{[18]} = 1.86$, $P < .05$). *Acacia tetragonophylla*, the posited ornithochore, showed a different pattern of SS establishment. Densities were significantly higher in the subcanopy than in open samples regardless of tree species, and slightly greater beneath *Atalaya* than under the somewhat less dense canopies of *A. aneura* (two-tailed $t_{[18]} = 2.06$, $P \approx .05$). Although these SS's were more numerous on average in the open quadrats near *Atalaya* than in those in the vicinity of *A. aneura*, this trend was not significant (two-tailed $t_{[18]} = 0.84$). Finally, at Camp David site II, SS densities of a second hypothesized ornithochore, *A. ligulata* (P1), were significantly greater beneath canopies of *A. aneura* than in open samples (Table 4).

At the three study localities on the Olive Downs Homestead, SS's of *Acacia aneura* were no more numerous on *Rhytidoponera* mounds than in quadrats positioned randomly off these mounds. The SS's of *A. tetragonophylla* tended to be associated with ant mounds only on the treeless plain at Stony Downs (for comparisons of numbers of individuals per ¼ m^2, $\bar{x} = 0.55$ on mounds vs. 0.00 off mounds; two-tailed $t_{[64]} = 3.60$, $P < .001$). Where canopy trees were abundant, SS's of *A. tetragonophylla* showed a significant association with the subcanopy microhabitat ($\bar{x} = 6.10$ vs. 1.60; one-tailed $t_{[38]} = 4.55$, $P < .0005$ at Downs Park and $\bar{x} = 4.90$ vs. 1.85; $t_{[38]} = 2.39$, $P < .025$ at Downs South), but no association with *Rhytidoponera* mounds ($t_{[58]} = 1.36$ and $t_{[32]} = 0.67$, respectively).

While we cannot compare the mean reproductive fitness of individuals in subcanopy and open micro-

TABLE 5. Chemical properties of soils from subcanopy and open microhabitats at Olive Downs Park, Sturt National Park, New South Wales. EC = electrical conductivity; P = bicarbonate-extractable phosphorus. N = no. samples.

Microhabitat	pH	EC (mS/cm)	Cl (mg/kg)	Na (mg/kg)	C (%)	NH_4 (mg/kg)	NO_3 (mg/kg)	P (mg/kg)	Exchangeable cations (mg/g)			
									Ca	Mg	K	Na
Subcanopy												
$\bar{x}$	6.5	0.07	53	12	0.67	10	3	22	0.42	0.10	0.20	0.02
SD	0.4	0.02	7	4	0.22	7	3	6	0.20	0.04	0.08	0.00
N	15	15	15	15	15	15	15	15	8	8	8	8
Open												
$\bar{x}$	6.5	<.06	<50	11	0.22	4	<3	15	0.38	0.14	0.16	0.02
SD	0.2	0.00	0	4	0.07	2	3	4	0.16	0.06	0.08	0.00
N	15	15	15	15	15	15	15	15	8	8	8	8

habitats, subcanopy plants as a group do not appear to be reproductively inhibited. Both total biomass and total fruiting biomass were greater on average in subcanopy than open plots (means of 175.9 cm^3 vs. 52.9 cm^3 for total plant volume, and 105.6 cm^3 vs. only 10.3 cm^3 for volume of fruiting plants). Only 19.5% of the biomass of plants in open microhabitats was fruiting, in comparison with 60.0% of subcanopy biomass.

Microhabitats and soils

Quantities of certain soil constituents were below the minimum threshold for which our analyses can give precise figures. Because the results of these analyses were reported to us as "less than that threshold value" (Table 5), and means were calculated using these threshold figures, means slightly overestimate levels of these nutrients (notably available nitrate and ammonium), especially in soils from open sites. However, in every case of statistically significant differences between microhabitat types, this biases against our finding of nutrient concentration in subcanopy soils.

The most pronounced differences in soils from the two microhabitat types are in content of available nitrogen and phosphorus (Table 5). Most of the additional nitrogen available to plants beneath tree canopies takes the form of ammonium (greater in the subcanopy by a factor of approximately 2; $P < .05$ in one-tailed sign test), but nitrates are also slightly more concentrated there (factor of ≈ 1.2; $P < .05$ in one-tailed sign test). Subcanopy soils are also richer in organic carbon (factor of >3; one-tailed $t_{[28]} = 7.50$, $P \ll .001$) and available phosphorus (factor of ≈ 1.5; one-tailed $t_{[28]} = 3.76$, $P \ll .001$). No other differences in physical and chemical properties of the soils are statistically significant.

DISCUSSION

Evolved dispersal syndromes

The Australian acacias provide an excellent opportunity to search for pattern and process in the molding of dispersal adaptations. The largely endemic subgenus *Phyllodineae* has radiated in comparative isolation to give high species richness and to dominate many habitats in arid Australia. Major dispersal syndromes are recognizable on the basis of just a few criteria (Table 6), some of which can be judged from herbarium specimens. Using herbarium specimens and criteria somewhat different from our own, D. O'Dowd and A. Gill (*personal communication*) are independently separating a different sample of *Acacia* species into the same major dispersal categories identified here. Although some dispersal of Australian acacias undoubtedly occurs independently of transport by ants or birds (see below), there is compelling evidence that many species have specialized adaptations for myrmecochory and ornithochory.

Probable myrmecochores are characterized by diaspores with relatively small, white or off-white arils of comparatively low energy reward, and may include the majority of Australian acacias. White arils are often (Pijl 1982) but not always (e.g., Skutch 1980) indicative of myrmecochory. Although ant vision is poorly studied (Wilson 1971), at least some ants are known to be attracted to white coloration against a black or dark background (Voss 1967). Most of our white-arillate species are typical of myrmecochorous plants in dropping their seeds on the ground or actively presenting them near ground level (reviewed in Berg 1975 and Pijl 1982). A variety of omnivorous and granivorous ants transport the diaspores of *Acacia*, and our observations confirm the generalization of Beattie et al. (1979) and Horvitz and Beattie (1980) that interactions between myrmecochorous plants and ants are often not highly specialized or species specific.

In contrast to diaspores with white arils, those with colored arils are eaten by birds. Avian consumers of fruits and arils rely extensively on color vision in locating food resources and often show preferences for reds and yellows (Turcek 1963, McDiarmid et al. 1977, Skutch 1980). Like the arils of the bird-dispersed *A. cyclops* (Glyphis et al. 1981) and a number of neotropical swollen-thorn acacias (Janzen 1969), those of Group II species here exhibit diaspores conspicuously in open pods, and the colored arils contrast sharply with black or brown seeds. Based on our sample of species, maximum diaspore size is greater in ornith-

TABLE 6. Characteristics of Group I and Group II *Acacia* species. E/WMD = (energy content of aril)/(wet mass of diaspore). SS = small shrub.

Trait	Group I	Group II
Probable dispersal syndrome	myrmecochory	ornithochory
Dispersal agents	ants	birds and ants
Diaspore presentation	scattered on ground	displayed on plant
Aril characters:		
Color	white or whitish-yellow	red, orange, or bright yellow
Ratio E/WMD	low	high
% lipid	low	high
% protein	(high)?	(low)?
Seed parasitism	high	low
SS occurrence	ant mounds (weak evidence)	under perch trees of birds and on ant mounds

ochorous than myrmecochorous acacias (Table 3). Longitudinal orientation of seeds in legumes is a strong correlate of ornithochory both in the species we studied and in an expanded sample shown in Table 7. Seed orientation may play a role in the display of diaspores from plants, but this hypothesis remains untested.

Evidence for avian exploitation of *Acacia* diaspores comes from the studies of Forde (*in press a* and *b*), who has both direct observations of birds feeding on *Acacia* diaspores and many records of undamaged *Acacia* seeds in the fecal samples of these birds (Tables 1 and 7). Forde has shown that at least two species in the Meliphagidae, the Singing Honeyeater (*Lichenostomus virescens*) and the Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*), are virtual specialists on the arils of certain acacias when and where diaspores are produced in abundance. Although Forde has established that both of these birds forage on diaspores of *A. tetragonophylla* and *A. ligulata*, probably only *L. virescens* is an important dispersal agent at our study site in Sturt National Park. The Singing Honeyeater is a year-round resident of this region, and its breeding season (August through December) overlaps the period of diaspore production in these two *Acacia* species (Wyndham 1978). In contrast, the Spiny-cheeked Honeyeater is a winter resident at our site and typically has migrated by the end of October, before diaspores here have matured (Wyndham 1978). Nevertheless, this species may be an important dispersal agent of *Acacia* in other parts of its range in the central and southern arid regions of Australia. Also consuming the diaspores of *A. ligulata* in other parts of its range are the Red Wattlebird (*Anthochaera carunculata*) and the Eastern Silvereye (*Zosterops lateralis*) (Forde, *in press a*). Finally, diaspores of other acacias with dispersal adaptations similar to those of our Group II species are also eaten by birds (Table 7 and Forde [*in press a* and *b*]).

Disparities in the food rewards of diaspores in species Groups I and II (Table 3 and Fig. 3) are consistent with the probable differences in the foraging costs of ants (cursorial ectotherms) and birds (flying endotherms). Not surprisingly, absolute investment in aril mass increases with diaspore mass, but Group I species (myrmecochores) typically provide less food reward per propagule than do Group II species (ornithochores) with diaspores of similar mass. Where Group I and Group II species do provision diaspores with similar ratios of E/WMD, species in the latter group supply arils with a greater percentage water content. This water may function as a supplemental reward to avian dispersal agents. However, we cannot rule out an alternative hypothesis, that the birds do not benefit significantly from the added water but are attracted to arils with relatively high water content because these appear larger and more valuable than they actually are. The four avian-dispersed species with greatest aril water content (species 4, 3, 2, and 5) occur across the northern arid zone (Maslin and Pedley 1982), where cyclonic summer storms result in relatively high mean annual rainfall. In contrast, *A. tetragonophylla* and *A. ligulata* are distributed throughout the more xeric central arid zone.

The chemical composition of arils in myrmecochores and ornithochores studied here is similar to that reported for other plants adapted for dispersal by ants (Bresinsky 1963) and birds (McDiarmid et al. 1977), respectively. The exception is the much lower aril water content of xerophytic Australian acacias (Table 3) in comparison with literature reports for two myrmecochorous mesophytic herbs of temperate forests (84.3 and 90.7%) and an ornithochorous rain forest tree (78.5%). Like our own data, those from McDiarmid et al. (1977) reveal a relatively large investment by ornithochores in energy-rich lipids, possibly essential attractants for dispersal agents with the high metabolic demands accompanying endothermy and flight. On average, protein content is slightly higher in the myrmecochorous acacias than in either ornithochorous acacias (this study) or ornithochorous tropical trees (10.9 and 15% in McDiarmid et al. 1977). While the energetic costs of foraging are probably lower for ants than for birds, ants probably channel a greater proportion of their resources directly into brood, and their demand for protein should be relatively high. Carroll and Janzen (1973) have argued that food bodies of myrmecochorous plants may mimic the chemical composition of the insect prey of ants. A number of the genera of ants listed in Table 1 are known to forage on insects or seeds that are likely to contain relatively high levels of protein.

Two factors suggest that dispersal adaptations are evolutionarily labile as selection pressures change over space and time. First, diaspores of at least one species, *A. ligulata,* exhibit geographic variation, resembling those of myrmechores in one population and those of ornithochores at a second locality. Second, dispersal modes are not taxonomically conservative features of the major systematic subdivisions of subgenus *Phyllodineae.* This is true whether we look only at the relatively few species included in our study, or whether we examine an expanded sample drawn from the literature and limited surveys of herbarium specimens. Table 7 lists, by sectional affiliation, a number of species whose diaspores and/or legumes mark them as probable ornithochores. (Space does not permit a listing of the many presumed myrmecochores identified in each section.) Of seven major taxonomic sections, the *Juliflorae, Plurinerves,* and *Phyllodineae* contain the majority of all species (≈190, 140, and 290, respectively [Maslin and Pedley 1982]). The ornithochorous phenotype is common in each of these sections (Tables 1 and 7 and Fig. 3). Within the section *Phyllodineae,* the *ligulata* complex of closely related species (some or all of which tend to intergrade into other members of the group, B. Maslin, *personal communication*) accounts for 10 of the 13 ornithochores listed for this section in Table 7.

Species that apparently lack functional arils also occur in the three major taxonomic sections. In *A. ramulosa,* relatively large seed size and low aril protein content separate this species from myrmecochores, while the very low ratio of E/WMD suggests that diaspores would be unattractive to birds. The aggregation of many weathered but unopened legumes beneath parent plants is also consistent with the apparent lack of adaptations for dispersal by ants and birds. Based on examination of herbarium specimens, absence of functional arils also occurs in the *Juliflorae* (*A. ramulosa* and *A. trachycarpa*), the *Phyllodineae* (*A. juncifolia* and *A. peuce*), and the *Plurinerves* (*A. anaticeps* and *A. cambagei*).

Despite the fact that evolved characteristics of *Acacia* species tend to mark them as specialists on either ants or birds as agents of dispersal, some species are clearly dispersed by various means. The four Group I species clustered within the dotted enclosure of Fig. 3 all have flat, papery legumes that may be widely dispersed by water as well as transported short distances by ants. In arid central Australia, *A. victoriae* occurs frequently along intermittent watercourses, where its seeds may be carried by water. The spherical shape and unusually thick seed testae of this species (Cavanaugh 1980) may be adaptive for this form of dispersal. Diaspores of many ornithochores are transported by ants as well as birds. Workers collect these diaspores avidly when offered in bait trays, gather naturally available diaspores (Table 1) and can influence the distribution of establishing seedlings. Finally, there is no necessary correlation between the number of seeds dispersed by a particular physical or biological agent and the value of that form of dispersal. Without data to evaluate the success of seeds dispersed by various agents, classifications based on morphological and chemical adaptations for dispersal probably give the best support (albeit indirect) for the importance of a particular dispersal mode.

TABLE 7. Posited ornithochores (by sectional affiliation within the subgenus *Phyllodineae*) based on the literature, herbarium specimens and this study. ND = no data.

Species	AC*	OSP*	Source†
Juliflorae			
auriculiformis	O	T	a
cowleana	Y	L	b
holosericea	Y	L	b
leptocarpa	Y	L	a
sophorae	WY	L	d (1, 2, 3, 5), f
pellita	Y	L	c
sessilispica	Y	L	c
solandri	ND	L	a
tenuissima	O	L	b
Phyllodineae			
ampliceps	RO	L	c
ashbyae	Y	L	c
bivenosa	R	L	c
ligulata	RY	L	b, d (1, 2, 3, 5), f
aff. *sclerosperma* (Shark Bay, West Australia)	O	ND	c
ligustrina	ND	ND	c
merrallii	Y	ND	c
rostellifera	RY	L	c
salicina	R	L	c, f
tetragonophylla	Y	L	b, d (1, 2)
tysonii	R	L	c
validinerva	YW	L	f
xanthina	Y	L	c
Plurinerves			
colletoides	Y	L	c, f
coriaceae	Y	L	c, f
melanoxylon	P	L	c, d (4, 5), f
nyssophylla	Y	ND	c, d (1)
oraria	R	L	a
oswaldii	YO	L	c, d (1, 2), f
roycei	ND	ND	c

* AC = aril colors; OSP = orientation of seed in pod. Designations for AC and OSP as in Table 1, and P = pink.

† Sources: a = Pedley 1975; b = this study; c = examination of herbarium specimens; d = Forde's evidence (*in press a* and *b*) that diaspores are taken by birds, including: (1) Singing Honeyeaters (*Lichenostomus virescens*); (2) Spiny-cheeked Honeyeaters (*Acanthagenys rufogularis*); (3) Red Wattlebirds (*Anthochaera carunculata*); (4) Yellow-faced Honeyeaters (*Lichenostomus chrysops*) and (5) Eastern Silvereyes (*Zosterops lateralis*); e = Glyphis et al. 1981; f = Whibley 1980. Species inclusions based on aril color, relative size of aril, and pod morphology.

Ecological correlates of dispersal

Our evidence for the role of dispersal in determining SS shadows is less than complete. SS's of the ornithochorous *A. tetragonophylla* are disproportionately abundant on nest mounds of *Rhytidoponera* sp. B as well as in subcanopy microhabitats. However, *A. aneura*, the single myrmecochore studied, is not associated with either of these sites. Diaspores of *A. tetragonophylla* are preferred over those of *A. aneura* by large ants in the genus *Rhytidoponera* (D. W. Davidson, *personal observation*). Arils of *A. aneura* offer a relatively low energy reward (Table 3 and Fig. 3), and we have observed only small-bodied ants in the genera *Melophorus* and *Pheidole* foraging for this species' diaspores. Because nest mounds of these ants are moved frequently (in sharp contrast to the long-lived *Rhytidoponera* mound microhabitats), we were unable to detect associations between any *Acacia* species and the mounds of these ants, though we did find seeds discarded in refuse heaps (Table 1). Experiments or long-term studies of marked nest positions (e.g., Majer 1982) will be necessary to elucidate the influence of *Melophorus* and *Pheidole* species on seedling shadows in myrmecochorous acacias.

The pattern of seedling establishment is probably affected both by dispersal and by microhabitat heterogeneity that determines growth and survivorship. An observation pointing to the importance of dispersal per se is the more pronounced association of *A. tetragonophylla* with *Rhytidoponera* mounds on the treeless plain (Table 4), where there are fewer birds than in neighboring habitats with greater vegetation height diversity (Wyndham 1978). Interestingly, *Rhagodia nutans* and *Enchylaena tomentosa*, two perennial saltbushes with fleshy red and yellow fruits, respectively, showed this same pattern of distribution across our study sites at Olive Downs (D. W. Davidson and S. R. Morton, *personal observation*). Some evidence indicates that mound and subcanopy sites may also represent especially favorable microhabitats. Both myrmecochorous and closely related nonmyrmecochorous chenopods growing on nest mounds of *Rhytidoponera* sp. B were much larger on average than conspecifics located off the mounds (Davidson and Morton 1981*b*). In comparison with nearby sites in the open, subcanopy microhabitats commonly show more luxuriant growth of *Acacia* and other plants such as the saltbushes *Enchylaena tomentosa*, *Rhagodia nutans*, and *Sclerolaena diacantha*, and more prolific fruiting in *A. tetragonophylla*.

Subcanopy and mound microhabitats share at least two attributes that may account for their favorable effect on plant establishment and growth and may ultimately account for the evolution of dispersal mechanisms that concentrate seeds in these locations. First, moisture stress may be less severe in these microhabitat types than in open microhabitats. Tree canopies shade plants from high midday temperatures and slow transpirational losses (Slatyer 1965). Rainfall penetration in the soil is greater in subcanopy than in open microhabitats, both because shade reduces evaporative losses (Pressland 1976), and because the characteristic growth form of mulga (*A. aneura*) channels rainfall down the tree trunk and allows greater moisture infiltration near its base (Slatyer 1961, 1965, Pressland 1978). Rainfall may also penetrate to a greater depth on ant mounds than in surrounding soil, because the excavation activities of ants reduce soil compaction (Davidson and Morton 1981*a*). Finally, the greater organic content of mound and subcanopy soils (see below) increases moisture-holding capacity of these soils. Mound soils from nests of *Rhytidoponera* sp. B at Fowlers Gap, New South Wales, absorb on average 1.7 times more water than do off-mound soils, after soils are oven-dried to constant mass, and they lose this water more gradually (D. W. Davidson, *personal observation*).

Nutrient availability is a second factor that may influence microhabitat favorability. Soils of the Australian arid zone are notably ancient, leached, and poor in mineral content, particularly in nitrogen and phosphorus content (Beadle 1966, Charley and Cowling 1968, Leeper 1970, Williams and Andrew 1970, Beard 1976). Favorable moisture conditions should facilitate nutrient uptake on ant mounds and subcanopy soils, but nutrients are also measurably more concentrated in these two microhabitats. While the discussion below emphasizes availability of nitrogen and phosphorus, other important elements probably have similar patterns of distribution.

A great deal of evidence has shown that nutrients are concentrated on the nest mounds of many ants. At Fowlers Gap, mean concentrations of phosphorus and available nitrogen are greater by factors of >3 and >200, respectively, in soils from mounds of *Rhytidoponera* sp. B than in off-mound soils nearby (Davidson and Morton 1981*a*). Briese (1982) has also documented concentration of nutrients and organic matter on the mounds of many omnivorous and granivorous ants in a saltbush shrubland in western New South Wales. Representatives of genera with relatively mobile nest entrances (e.g., *Pheidole*, *Chelaner*, and *Melophorus*) probably concentrate nutrients to a lesser degree than does *Rhytidoponera* sp. B, though this cannot be judged adequately from Briese's small sample sizes. Nest surfaces of ants in the *Iridomyrmex purpureus* species complex are distinctive in being formed from deep, nutrient-poor soils (Briese 1982) and are typically barren of vegetation (Ettershank 1971). These species collect the diaspores of several *Acacia* species (Table 1) and may be parasites of the mutualistic interactions between ants and plants.

Our data demonstrate that available forms of nitrogen and phosphorus and organic carbon are also concentrated (though to a lesser degree) beneath the canopies of nurse trees. Several factors may be involved in producing this nutrient mosaic. First, the large contribution of ammonium to available nitrogen in subcanopy soils suggests that nutrients may accumulate here via transport to these microhabitats by kangaroos. At Camp David site I in Sturt National Park, the fecal pellets of kangaroos were on average nine times more concentrated in the subcanopy than in open areas nearby (D. W. Davidson and S. R. Morton, *personal observation*). Nitrogen transport to these microhabitats through urination could be of even greater magnitude; depending on diet, kangaroos may lose up to six times more nitrogen daily through urination than through defecation (McIntosh 1966). Because kangaroo populations in Sturt National Park are artificially high and exceed those in most other parts of arid Australia (Caughley et al. 1980), nitrogen may be somewhat more concentrated in subcanopy microhabitats on our study plots than in other areas of the Australian arid zone. Conditions promoting the mineralization of nutrients may also enhance nutrient availability in subcanopy soils. Carbon/nitrogen ratios favorable for nitrification occur beneath trees and shrubs as a result of litter accumulation (Perry 1970, Rixon 1971). The greater soil moisture in this microhabitat can promote both the mineralization of nutrients (e.g., Rixon 1968) and root nodulation in the presence of appropriate rhizobia (Beadle 1964). Finally, ornithochorous plants may obtain a nutrient advantage in the early stages of establishment simply by association with bird feces (Noble 1975, Glyphis et al. 1981). Relatively high nutrient levels may be most crucial for *Acacia* during this early (prenodulation) stage.

Elsewhere (Davidson and Morton 1981*a*), we have suggested that the high frequency of myrmecochory in the Australian flora (e.g., Berg 1975) may reflect natural selection favoring plants that direct their seeds to nutrient-rich microhabitats, in a background of generally poor soil quality. Myrmecochory has been demonstrated or inferred in many important arid zone plants, including a number of semiperennial saltbushes (Chenopodiaceae; Davidson and Morton 1981*a*) and grasses in the genera *Ichnanthus* (P. Latz, *personal communication*) and *Triodia* (Sernander 1906). Thus, its occurrence in *Acacia*, the dominant genus of arid zone trees and shrubs, is not unexpected. Similarities between microhabitats colonized by ant-dispersed and bird-dispersed propagules could have facilitated evolutionary transition from myrmecochory to ornithochory. In addition to *A. tetragonophylla*, at least two other species with red and yellow (*Enchylaena tomentosa*) and red (*Rhagodia nutans*) fruits tend to grow in association with both ant mounds and subcanopies of nurse trees (D. W. Davidson and S. R. Morton, *personal observation*). Because concentration of seeds in favorable microhabitats could increase their susceptibility to vertebrate seed predators, the insignificance of small mammals as granivores in the Australian arid zone (Morton 1979) may have been an important additional factor facilitating the evolution of these forms of dispersal (Davidson and Morton 1981*a*).

Although both myrmecochory and ornithochory may function to position seeds in environments favorable for seedling establishment, the extent to which selection favors one syndrome of dispersal adaptations over another should depend on the relative costs and benefits of these adaptations to individuals of a particular species. Endothermy and flight are energetically demanding, and plants expend more energy per milligram of propagule for bird dispersal than for dispersal by ants. The greater cost of provisioning diaspores for ornithochory may be counterbalanced by one or more of several advantages. We consider two possible advantages below.

First, parasitoid loads are lower on average in seeds of avian-dispersed (i.e., Group II) acacias. Janzen (1969) suggested that many seeds of neotropical bird-dispersed acacias may escape mortality from seed parasitoids, because the larvae of bruchids (Coleoptera, Bruchidae) are destroyed in the avian digestive tract before the viability of infested seeds is impaired. Under Janzen's explanation, rates of parasitoid infestation may be low or high, but larvae cause little damage to seeds in either case. We must postulate a slightly different mechanism for two reasons. First, we measured different levels of damage to the seeds of myrmecochores and ornithochores prior to removal of seeds by ants or birds. Thus, rates of parasitoid infestation must be generally lower in ornithochores than in myrmecochores. Second, the seed parasitoids we detected either caused seed abortion at early stages of development or were nearing emergence at the time plants were displaying mature diaspores. There are few indigenous bruchids in Australia (Southgate 1978), and both our results and those of Preece (1971*a, b*) suggest that chalcid wasps are prominent seed parasitoids of *Acacia* here. In contrast to many bruchids, chalcid larvae tend to develop in very young seeds (Malyshev 1968). We hypothesize that the low parasitoid loads in seeds of bird-dispersed Australian acacias may occur because high predation on parasitoids by avian dispersal agents during previous fruiting seasons helps to maintain generally low parasitoid populations and low rates of seed infestation. In comparison to birds, the large omnivorous ants and relatively small granivores that we observed transporting *Acacia* seeds may be slower to remove diaspores and unable to crack the hard seed testae to extract parasites. This hypothesis is tenable only if parasitoid populations are highly localized to particular host plants in successive years.

Second, ornithochorous acacias may benefit from subsidiary dispersal by ants under certain circumstances. Dispersal by ants may be particularly important where a paucity of adult trees results in reduced bird densities or during the early establishment of populations when fruiting biomass may be inadequate to attract birds. Birds may occasionally or even regularly drop seeds from their perches with part of the aril still attached. Since ants collect the diaspores of *A. tetragonophylla* and *A. ligulata* (P1) even after most of the aril has been removed, plants may benefit from two-stage dispersal that positions seeds on ant nests beneath trees. Because of the ubiquity of large *Rhytidoponera* in arid Australia (Greenslade 1979), some dispersal should occur to satisfactory microhabitats despite spatial and temporal patchiness in the availability of avian dispersal agents. In the final analysis, however, only long-term experimental studies will enable us to understand the benefits that acacias derive from seed dispersal by ants and birds.

In recent years, concern has arisen over the widespread failure of establishment in some dominant arid zone perennials (Hall et al. 1964, Charley and Cowling 1968, Preece 1971*a*, Burrows 1973, Crisp and Lange 1976, Moore 1976, Lange and Willcocks 1980). Geographically, the distribution of *A. aneura* has contracted during recent history (Nix and Austin 1973). Crisp (1978) reports that even after release from grazing, regeneration of mulga requires an exceptional sequence of climatic events. Dispersal interactions can have considerable impact on the local distribution and abundance of various plants (Beattie and Culver 1981, Davidson and Morton 1981*a*, and this paper). Our data suggest that the establishment of some common arid zone perennials depends on microenvironmental conditions that may be permanently altered by disturbing populations of dispersal agents, by destroying adult trees, or by allowing these trees to die without replacement because of heavy grazing pressure. Management practices designed to encourage regeneration of the arid zone flora should take into account the ecology of dispersal and early establishment.

ACKNOWLEDGMENTS

We thank B. Maslin, L. Pedley, and S. Jacobs for identifying plant specimens, and R. Taylor and P. J. M. Greenslade for taxonomic assistance with ants. A. Beech provided invaluable assistance in arranging for soil analyses. C. Carter and D. McKey facilitated our work at Fowlers Gap Research Station and the Northern Territory Herbarium, respectively. B. Cole, P. Coley, D. Janzen, B. Maslin, L. Pedley, and editor R. Cruden provided helpful comments on an earlier draft of the manuscript. We are especially indebted to B. Maslin for the hospitality and guidance he offered during our visit to the Western Australian Herbarium, and to N. Forde, who generously took time to show us his field operations. This research was supported by National Science Foundation grant INT 80-10801 to both authors, by an Ian Potter Foundation travel grant and University of Utah Faculty Development Award to D. W. Davidson and a University of Sydney Postdoctoral Fellowship and Australian Research Grants Committee award to S. R. Morton. Finally, we wish to thank the personnel of the National Parks and Wildlife Service of New South Wales for their courtesy and support as well as their foresight in protecting Sturt National Park from grazing, so that studies like ours are possible.

LITERATURE CITED

Beadle, N. C. W. 1964. Nitrogen economy in arid and semi-arid plant communities. III. The symbiotic nitrogen-fixing organisms. Proceedings of the Linnean Society of New South Wales **89**:273–286.

———. 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology **47**:992–1007.

Beard, J. S. 1976. The evolution of Australian desert plants. Pages 51–63 *in* D. W. Goodall, editor. Evolution of desert biota. University of Texas Press, Austin, Texas, USA.

Beattie, A. J., and D. C. Culver. 1981. The importance of myrmecochory in the herbaceous flora of West Virginia forests. Ecology **62**:107–115.

Beattie, A. J., D. C. Culver, and R. J. Pudlo. 1979. Interactions between ants and the diaspores of some spring flowering herbs in West Virginia. Castanea **44**:177–186.

Berg, R. Y. 1975. Myrmecochorous plants in Australia and their dispersal by ants. Australian Journal of Botany **23**: 475–508.

Bresinsky, A. 1963. Bau, Entwicklungsgeschichte und Inhaltsstoffe der Elaiosomen. Bibliotheca Botanica **126**.

Briese, D. T. 1982. The effect of ants on the soil of a semi-arid saltbush habitat. Insectes Sociaux **29**:375–382.

Brody, S. 1945. Bioenergetics and growth. Reinhold, New York, New York, USA.

Burrows, W. H. 1973. Regeneration and spatial patterns of *Acacia aneura* in southwest Queensland. Tropical Grasslands 7:57–68.

Carroll, C. R., and D. H. Janzen. 1973. Ecology of foraging by ants. Annual Review of Ecology and Systematics **4**:231–258.

Caughley, G., G. C. Grigg, J. Caughley, and G. J. E. Hill. 1980. Does dingo predation control the densities of kangaroos and emus? Australian Wildlife Research **7**:1–12.

Cavanaugh, A. K. 1980. A review of some aspects of the germination of acacias. Proceedings of the Royal Society of Victoria **91**:161–180.

Charley, J. L., and S. W. Cowling. 1968. Changes in soil nutrient status resulting from overgrazing and their consequence in plant communities of semi-arid areas. Proceedings of the Ecological Society of Australia **3**:28–38.

Crisp, M. D. 1978. Demography and survival under grazing of three Australian semi-desert shrubs. Oikos **30**:520–528.

Crisp, M. D., and R. T. Lange. 1976. Age structure, distribution and survival under grazing of the arid-zone shrub *Acacia burkettii*. Oikos **27**:86–92.

Davidson, D. W., and S. R. Morton. 1981*a*. Myrmecochory in plants (F. Chenopodiaceae) of the Australian arid zone. Oecologia (Berlin) **50**:357–366.

Davidson, D. W., and S. R. Morton. 1981*b*. Competition for dispersal in ant-dispersed plants. Science **213**:1259–1261.

Ettershank, G. 1971. Some aspects of the ecology and nest microclimatology of the meat ant, *Iridomyrmex purpureus* (Smith). Proceedings of the Royal Society of Victoria **84**: 137–151.

Forde, N. *In press a.* Fruit-eating birds of temperate Australia. *In* H. Ford and D. Paton, editors. Coevolution of birds and plants in southern Australia. Government Printers, Adelaide, South Australia, Australia.

———. *In press b.* Nectar and fruit feeding birds. *In* H. R. Wallace, editor. The ecology of South Australia's forests and woodlands. Government Printers, Adelaide, South Australia, Australia.

Glyphis, J. P., S. J. Milton, and W. R. Siegfried. 1981. Dispersal of *Acacia cyclops* by birds. Oecologia (Berlin) **48**: 138–141.

Greenslade, P. J. M. 1979. A guide to ants of South Australia. South Australian Museum, Adelaide, South Australia, Australia.

Hall, E. A. A., R. L. Specht, and C. M. Eardley. 1964. Regeneration of the vegetation on Koonamore Vegetation Reserve, 1926–62. Australian Journal of Botany **19**:21–49.

Horvitz, C. C., and A. J. Beattie. 1980. Ant dispersal of *Calathea* (Marantaceae) seeds by carnivorous ponerines (Formicidae) in a tropical rain forest. American Journal of Botany **67**:321–326.

Janzen, D. H. 1969. Birds and the ant x *Acacia* interaction in central America, with notes on birds and other myrmecophytes. Condor **71**:240–256.

Janzen, D. H., and P. S. Martin. 1982. Neotropical anachronisms: the fruits the Gomphotheres ate. Science **215**:19–27.

Lamprey, H. F. 1967. Notes on the dispersal and germination of some tree seeds through the agency of mammals and birds. East African Wildlife Journal **5**:179–180.

Lamprey, H. F., G. Halevy, and S. Makacho. 1974. Interactions between *Acacia,* bruchid seed beetles and large herbivores. East African Wildlife Journal **12**:81–85.

Lange, R. T., and M. C. Willcocks. 1980. Experiments on the capacity of present sheep flocks to extinguish some tree populations of the Southern Australian arid zone. Journal of Arid Environments **3**:223–229.

Leeper, G. W. 1970. Soils. Pages 21–31 *in* G. W. Leeper, editor. The Australian environment. Commonwealth Scientific and Industrial Research Organization, Melbourne University Press, Melbourne, Victoria, Australia.

Majer, J. D. 1982. Ant-plant interactions in the Darling Botanical District of Western Australia. Pages 63–66 *in* R. Buckley, editor. Ant-plant interactions in Australia. Junk, The Hague, The Netherlands.

Malyshev, S. I. 1968. Genesis of the Hymenoptera and the phases of their evolution. Methuen, London, England.

Maslin, B. R., and L. Pedley. 1982. The distribution of *Acacia* (Leguminosae: Mimosoidae) in Australia. Parts 1 and 2. Western Australian Herbarium Research Notes **6**: 1–171.

McDiarmid, R. W., R. E. Ricklefs, and M. S. Foster. 1977. Dispersal of *Stemmadenia donnell-smithii* (Apocynaceae) by birds. Biotropica **9**:9–25.

McIntosh, D. L. 1966. The digestibility of two roughages and the rates of passage of their residues by the red kangaroo, *Megaleia rufa* (Demarest), and the Merino sheep. Commonwealth Scientific and Industrial Research Organization Wildlife Research **11**:125–135.

Moore, P. D. 1976. Influence of grazing. Nature **262**:6–7.

Morton, S. R. 1979. Diversity of desert-dwelling mammals: a comparison of Australia and North America. Journal of Mammalogy **60**:253–264.

Nix, H. A., and M. P. Austin. 1973. Mulga: a bioclimatic analysis. Tropical Grasslands **7**:9–21.

Noble, J. C. 1975. The effects of emus (*Dromaius novaehollandiae* Lathum) on the distribution of the nitre bush (*Nitraria billardieri* DC.). Journal of Ecology **63**:979–984.

Pedley, L. 1975. Revision of the extra-Australian species of *Acacia* subgenus *Heterophyllum.* Contributions of the Queensland Herbarium **18**:1–24.

Perry, R. A. 1970. The effects on grass and browse production of various treatments on a mulga community in Central Australia. Pages 63–66 *in* Proceedings of the Eleventh International Grasslands Congress. University of Queensland Press, St. Lucia, Queensland, Australia.

Pijl, L. van der. 1982. Principles of dispersal in higher plants. Springer-Verlag, New York, New York, USA.

Preece, P. B. 1971*a*. Contributions to the biology of mulga. I. Flowering. Australian Journal of Botany **19**:21–38.

———. 1971*b*. Contributions to the biology of mulga. II. Germination. Australian Journal of Botany **19**:39–49.

Pressland, A. J. 1976. Soil moisture distribution as affected by throughfall and stemflow in an arid zone shrub community. Australian Journal of Botany **24**:641–649.

———. 1978. Soil moisture distribution and evapotranspiration of a mulga (*Acacia aneura* F. Muell.) scrubland in southwestern Queensland. Pages 129–137 *in* K. M. W. Howes, editor. Studies of the Australian arid zone III. Water in rangelands. Commonwealth Scientific and Industrial Research Organization, Melbourne, Victoria, Australia.

Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pages 152–292 *in* R. A. Paynter, editor. Avian energetics. Publications of the Nuttall Ornithological Club, Cambridge, Massachusetts, USA.

Rixon, A. J. 1968. Oxygen uptake and nitrification at various moisture levels by soils and mats from irrigated pastures. Journal of Soil Science **19**:55–66.

———. 1971. Oxygen uptake and nitrification by soil within a grazed *Atriplex vesicaria* community. Journal of Range Management **24**:435–438.

Ross, J. H. 1981. An analysis of the African *Acacia* species: their distribution, possible origins and relationships. Bothalia **13**:389–413.

Sernander, R. 1906. Entwurf einer Monographie der europaischen Myrmekochoren. Kungliga Svenska Vetenskapsakademiens Handlingar **41**:1–407.

Skutch, A. F. 1980. Arils as food of tropical American birds. Condor **82**:31–42.

Slatyer, R. O. 1961. Internal water balance of *Acacia aneura* F. Muell. in relation to environmental conditions. Arid Zone Research **16**:137–146.

———. 1965. Measurement of precipitation interception by an arid zone plant community (*Acacia aneura* F. Muell.). Arid Zone Research **25**:181–192.

Smith, D. 1969. Removing and analyzing total nonstructural carbohydrate from plant tissues. Wisconsin Agricultural Experimental Station Report **41**.

Southgate, B. J. 1978. Variation in the susceptibility of African *Acacia* (Leguminosae) to seed beetle attack. Kew Bulletin **32**:541–544.

Turcek, F. J. 1963. Color preferences in fruit and seed-eating birds. Proceedings International Ornithological Congress **13**:285–292.

Vassal, J. 1971. Contribution a l'étude morphologique des graines d'acacia. Bulletin de la Societe d'Histoire Naturelle de Toulouse **107**:191–246.

Voss, C. 1967. Uber das Formensehen der roten Waldameise (*Formica rufa*—Gruppe). Zeitschrift für vergleichende Physiologie **55**:225–254.

Whibley, D. J. E. 1980. Acacias of South Australia. D. J. Woolman, Goverment Printer, Adelaide, South Australia, Australia.

Williams, C. H., and C. S. Andrew. 1970. Mineral nutrition of pastures. Pages 321–348 *in* A. M. Moore, editor. Australian grasslands. Australian National University Press, Canberra, Capital Territory, Australia.

Wilson, E. O. 1971. The insect societies. Belknap Press, Harvard University Press, Cambridge, Massachusetts, USA.

Wyndham, E. 1978. Birds of the Milparinka district and Cooper Creek Basin. Emu **78**:179–187.