CHAPTER 4: DEMOGRAPHY OF *CRATAEGUS MONOGYNA* AND *PRUNUS MAHALEB*

4.1 Introduction and literature review

The link between biological invasions and population dynamics has not received a great deal of attention (Mack 1985). Some recent examples include theoretical papers by Bazzaz (1986), Crawley (1986) and Noble (1989) and a specific example by Vitousek and Walker (1989) of *Myrica faya* in Hawaii. Mack (1985, 128) suggested that "In addition to providing seemingly rapid and measurable examples of population growth, plant invasions allow precise assessment of a) the circumstances surrounding range expansion, and in turn, population growth; (b) the potential for competition between aliens and natives; and (c) extinctions". It is in the context of a) above that the present study is undertaken to examine the role of population dynamics in the determination of invasiveness of *C.monogyna and P. mahaleb.*

4.1.1 Population models

The basic population parameters used for describing populations are birth, death, immigration and emigration (Begon and Mortimer 1986 Harper and White 1974). The general relationship between them is expressed in the form of:

$$N_{t+1} = N_t + B - D + I - E \qquad (1)$$

where N_t is the number of individuals at time t, N_{t+1} is the number of individuals after one time interval, B is the number of births, D is the number of deaths, I is the number of immigrants and E is the number of emigrants occurring between t and t+1 (Begon and Mortimer 1986).

Linear models of continuous population growth exemplified by and Pearl and Reed (1920) take the form:

$$dN/dt = rN[(K-N)/K] \qquad (2)$$

Where the rate of growth of the population equals the potential rate of increase of the population per unit time, multiplied by the degree to which the population N falls short of its maximum attainable value K (Harper 1977). The integrated form of equation 2 takes the form of

$$N_t = N_0e^{rt} \qquad (3)$$

These linear models oversimplify population dynamics. They do not adequately deal with inherent variations within populations, specifically different sexes, sizes, ages and mortality and fecundity of individuals within a population (Caswell 1989).

The extension of simple population models to include individual variation explicitly recognizes the possibility to segregate like individuals into groups. The conceptually most simple grouping is a population segregated into age classes (this holds for organisms that reproduce at discrete times, e.g. seasonal reproduction in plants (Caswell 1989)). Depending on the time interval used (e.g. day, week or year), after one time interval (t+1) all surviving individuals will have aged one time interval. The number of individuals entering a new class will be directly proportional to the number in the previous age group. For the total population after one time interval, N_{t+1} will be a product of the initial population N_0 and survival rate P (Caswell 1989) such that

$$N_{t+1} = PN_0 \tag{4}$$

If the population is viewed as comprising individuals in n discrete classes then

$$N_t = n_{t1} + n_{t2} + n_{t3} + \ldots n_{tn-1} + n_{tn} \tag{5}$$

An extension of equation (5) expresses the proportion of individuals in each class at t+1 so that N_{t+1} is the sum of n classes at t+1 and is related to the survival of individuals from time t (Caswell 1989) such that

$$\begin{aligned} n_{t+1\ 1} &= P_1 n_{t1} \\ n_{t+1\ 2} &= P_2 n_{t2} \\ n_{t+1\ 3} &= P_{3t3} \end{aligned} \tag{6}$$

therefore

$$N_{t+1} = P_1 n_{t1} + P_2 n_{t2} + \ldots P_n n_{tn} \qquad (7)$$

This form of expressing population change soon becomes unwieldy. The inclusion of fecundity schedules F into the equation further exacerbates the complexity of describing population change. The number of offspring added to the first age class is proportional to the number of individuals in each reproductive class; each with their characteristic fecundity rate. Therefore F for the entire population after one time interval will be the sum of the products F_n fecundity rate for each class n and the number of individuals in each reproductive class P_n (Begon and Mortimer 1986, Caswell 1989).

4.1.2 Development of matrix models of population growth

Caswell (1989) and other researchers (e.g. Enright and Ogden 1979, Enright and Watson 1991) documented the development of a matrix approach to simplifying calculation of population change by regarding population changes after one time interval as a series of linear equations that relate to defined age classes. Lewis (1942) and Leslie (1945) independently developed a matrix approach to population modelling. A column vector of dimension 1 x n representing a population divided into n classes is premultiplied by a transition matrix representing survivorship and fecundity of individual classes derived from life-table data of vital rates.

Lefkovitch (1965) modified Leslie's methods of age analysis to include stage. One important reason for this development was that it is inherently difficult to observe individuals and estimate their age (Harper 1977, Caswell 1989). However a stage can be relatively easy to recognize (e.g. small, medium, large or pre-reproductive, reproductive, post-reproductive). More importantly, many biological schedules of reproduction and survival are determined by stage rather than age (e.g. Werner 1975, Harper 1977, Klinkhamer *et al.* 1987).

Matrix models involve some important assumptions that are inherently unrealistic. The transition matrix A of survival and fecundity rates is continually post multiplied by the population vector. Fecundity and survival remain constant throughout successive iterations. This is unrealistic as the environments in which populations find themselves vary over time; therefore survival and reproduction also vary (Caswell 1989). Catastrophic events (e.g. floods, fires, storms) which have a large influence on biological processes are not usually factored into matrix models. Density dependent factors are generally not taken into consideration, even though many plant species show an inverse relationship between survival and density (e.g. -3/2 thinning law, see Harper 1977).

An outcome of matrix models is exponential growth with no allowance for feedback mechanisms to regulate population growth. This implies limitless and inexhaustible environmental resources, clearly an unrealistic assumption in most situations. The matrix model also produces a stable population where the proportion of individuals in one size class to the next, between successive generations, will remain constant. That is the population increases at a constant rate such that

$$n_{1n}:n_{1n-1} = n_i:n_{2n-1} = n_i:n_{3n-1} \qquad (8)$$

and occurs irrespective of the initial population vector (Caswell 1989).

Despite these shortfalls the Leslie matrix approach utilizing age- and stage-classes has found a permanent place in population modelling. Matrix models can incorporate sex and geographical variation, mix modes of reproduction, and be applied to both animal and plant populations (Caswell 1989). The important point to keep in mind is that matrix models **only project** populations given a set of vital rates and in no way can it been seen to predict what a population will look like in the future (Caswell 1989).

As Mack (1985) suggested biological invaders may provide important subjects for population modelling. The nature of biological invasions overcome some of the weaknesses of matrix models outlined above. A biological invader is a new organism in a new environment. To the invader the resources of the new environment may indeed, for a time, be regarded as inexhaustible and limitless. Any population growth is also likely to be exponential. This modelling approach also allows for both positive (successful invasion) and negative (unsuccessful invasion) growth.

The construction of matrix models is covered in detail in section 4.1.5.

4.1.3 Modelling of long-lived perennials

Ideally population models should study entire populations. All individuals are followed from their birth to their death. Early population ecologists did precisely that by monitoring known populations of microorganisms with lifespans of hours and days in confined environments (e.g. Volterra 1931). Some plant population ecologists followed suit and studied short-lived annuals. However plant ecologists face an important limitation. The life span of larger organisms, especially many woody plants, approach and exceed the lifespan of researchers. This stumbling block has generally precluded really detailed population studies on them (Harper 1977).

There is a considerable number of demographic studies based upon herbaceous and other small, short-lived plants (e.g. Sarukhan and Gadgil 1974, Bierzychudek 1982, Werner and Caswell 1977) and many on trees and forests (e.g. Enright and Ogden 1979, Burns and Ogden 1985, Hartshorn 1975, Namkoong and Roberds 1974, Usher 1966). However Harper (1977) and Crawley (1990) identified a lack of demographic data for smaller woody plants (shrubs). They are "... for the most part...as difficult subjects for population biology as the most difficult trees" (Harper 1977, 636). Clonal growth in shrubs is an acute problem for demographers (Harper 1977). In the light of this, a comprehensive and comparative study might be expected to aid significantly a better understanding of shrub population dynamics.

4.1.4 Modelling of shrub populations

Demographic studies of shrub populations vary and include contrasting communities (Harper 1977). Chew and Chew (1965) studied *Larrea tridentata* (Creosote bush) in Arizona USA, Flower-Ellis (1971) researched *Vaccinium myrtillus* (Bilbery) in Sweden, and Pelton (1953) worked on *Symphoricarpos occidentalis* (Snowberry) in Minnesota. Later works include Burns and Ogden (1985) on *Avicennia marina* in New Zealand; van der Maarel, Boot, van Dorp and Rijntjes (1985) and van de Maarel, de Cock and de Wildt (1985) on successional changes in shrubs and trees on sand dunes in the Netherlands; Auld and Myerscough (1986) and Auld (1986, 1987) who studied the population dynamics of *Acacia suaveolens* in Australia; Lonsdale *et al.* (1989) on *Mimosa pigra* in the Northern Territory of Australia; and Smith and Harlen (1991) on *Cytisus scoparius* in northern New South Wales, Australia. These studies addressed a range of components of shrub populations including age and size of plants, rate of growth, seed bank dynamics and response to fire.

Woody plant demographic data consists predominantly of height and circumference measurements (Harper 1977, Ogden 1985). These have been widely used to describe the physical structure of individuals with the aim to describe the age structure of the population. However size is a poor determinant of age, as while a large plant may indeed be old, a small plant may be of any age (Harper 1977) depending upon growth and competition with respect to resource capture during the plant's development and the degree of herbivory it may suffer.

Size (stage) is often a better population parameter than age as phenological timetables are more dependent upon size and more in tune with other population parameters such as reproduction. Age is still an important parameter and may indirectly and perhaps inaccurately be obtained by size-age correlation using annual growth rings from a sample and applying this to the population as a whole. Destructive harvesting of all plants under study can provide accurate ages and sizes for each individual but can only be done at the completion of a study.

Harper (1977, 636) stated "any population biology that has hopes of explaining and predicting events must record the life of individuals..." To overcome the problems of modelling long-lived woody plants, regular censusing of individuals in a population over a period of years can be used to calculate growth rates and survival of individuals. This data can then be used to construct life-table schedules. The construction of a lifetable for a specific population involves following individual plants and monitoring growth, reproduction, birth and death and then grouping the individuals into distinct classes based on age or size. Transition probabilities between the various classes can be calculated from average growth rates and allow modelling of individuals passing through developmental stages from birth to death.

4.1.5 Construction of matrix models

In the matrix model numbers appear in columns and rows. These numbers represent life-table data which describe survival rates of each different age class, and reproductive rates. This matrix is called the transition or life-table data matrix and is denoted A (Begon and Mortimer 1986, Caswell 1989).

A population that can be divided up into discrete age or size classes can be represented by a singe column vector called a population matrix denoted as n. By multiplying the transition matrix by the population matrix we can project what the population may look like in the next generation. Thus one multiplication step gives the new population structure after one generation. If we then multiply this population with the transition matrix we have the population structure after two generations and so on.

Thus if A = Transition or life-table data matrix
n_t = population vector matrix at time t, then

$$A \times n_0 = n_1 \quad \text{and} \quad A \times n_1 = n_2 \ldots\ldots A \times n_{t-1} = n_t \qquad (9)$$

where n_0 is the initial population, n_1 is the population after one time interval and so on.

For populations grouped into age classes the transition matrix is set up from life-table data as follows: fecundity values F_n in table 4.1 are entered into the first row of the matrix in table 4.2; survival rates P_n are entered in as a diagonal in table 4.2.

Table 4.1 Hypothetical life-table data grouped into age classes.

	Age class				
	1	2	3	4	etc.
Fecundity	F_1	F_2	F_3	F_4	"
Survival	P_1	P_2	P_3	P_4	"

Table 4.2 Hypothetical transition matrix constructed from fecundity and survival values from table 4.1

F_1	F_2	F_3	F_4	.	.	F_n
P_1	0	0	0	.	.	.
0	P_2	0	0	.	.	.
0	0	P_3	0	.	.	.
0	0	0	P_4	.	.	.

The population matrix is a single column (see table 4.3) where n_1 = number of individuals in age class 1, n_2 = number of individuals in age class 2 and so on.

Table 4.3. Population matrix divided into n classes

n_1
n_2
n_3
n_4

Tables 4.2 and 4.3 describe an age classified model where survival of an individual means a progression to the next age class. The formulation of a stage classified model requires modification of the matrix to include a major diagonal element describing the survival of individuals which remain in the same size class P_n and a sub diagonal element which describes the transition of individuals into the next size class G_n (Caswell 1989). This is shown in table 4.4.

Table 4.4 The form of a size classified transition matrix for a population divided into five size classes (adapted from Caswell 1989).

P_0	F_1	F_2	F_3	F_4
G_0	P_1	0	0	0
0	G_1	P_2	0	0
0	0	G_2	P_3	0
0	0	0	G_3	P_4

The construction of transition matrices for *C.monogyna* and *P.mahaleb* follows the methods outlined by Caswell (1989), Enright and Ogden (1979), Burns and Ogden (1985) and Enright and Watson (1991).

The elements of the size classified matrix are derived from life-table data in the following way. Fecundity values are entered in the top row. The main diagonal elements P_n are obtained by multiplying survival rates by the proportion of individuals remaining in the same size class. The first subdiagonal elements G_n are derived by multiplying survival rates by the proportion of individuals moving into the next size class (Caswell 1986, Burns and Ogden 1985). The proportions of individuals remaining in the same size class or moving into the next class are derived from estimates of the initial population that, given average growth rates, move between size classes (see Burns and Ogden 1985). For populations which reproduce vegetatively, the inclusion of a second row of elements V_n immediately below the fecundity values describe the production of second size class individuals rather than seeds (Enright and Ogden 1979).

The matrix model can also be used to find λ (lambda) the finite rate of natural increase. λ is equal to the dominant latent root or eigenvalue of the transition matrix. The same value can be determined by iterative multiplication (see 4.1.11) until the proportions between successive generations remain unchanged (anywhere between 50 and 256 iterations (Caswell 1989)). For $\lambda<1$ a population is said to be in decline. For $\lambda>1$ the population is exponentially increasing and $\lambda=1$ the population is stable. λ is related to the intrinsic rate of natural increase r such that

$$r = \ln \lambda \tag{10}$$

where ln is the natural logarithm.

4.1.6 Population dynamics of biological invaders

Researchers have for many years tried to identify what population characteristics are common to invading organisms. The seminal work of Baker (1965) on the characteristics of the ideal weed has provided much of the impetus for succeeding studies. Roy (1990) outlined the properties of invading populations drawing on the work of Baker (1965) and Newsome and Noble (1986). In essence invaders are likely to have one or more 'weedy' characteristics. However the possession of some or all such characteristics will not ensure that a plant will be a successful invader (Roy 1990).

One avenue of research has focussed on the differences displayed by populations of an invading plant species between its home environment where it is not invasive and its new invaded environment where it is invasive.

Noble (1989) suggested the success or otherwise of an invading plant is related to certain demographic components of its population. If the invader population is assumed to be in equilibrium in its native habitat, the intrinsic rate of population increase is 1.0, and it has a stable age population structure, then a relatively simple relationship exists:

$$fvem/[(1-s)(1-j)(1-a)] = 1 \qquad (11)$$

where s is the rate of seed survival over a year, e is the rate of establishment, j is the rate of juvenile survival, m is the rate of maturation of juveniles, a is the adult survival rate and r is the reproductive output of adults which is a function of f the flowering effort and v which is related to all reproductive losses between flowering and the seed pool. Noble (1989) argued that if the invaded and source environments are indeed similar then s, a, j and f are largely genetically determined and remain similar in both environments.

If any one of v, e or m increases in the invaded environment then f will likely become excessive, upsetting the equilibrium of the species, and population growth will become rapid. If there is also effective local dispersal of propagules a plant is likely to become an invader (Noble 1989, Bazzaz 1986). A large seeding effort may therefore be seen as a sign of potential for a species to become invasive. Given similarities in the abiotic components of the source and invaded environments then invasion success will likely be determined in the main by biotic factors especially those relating to dispersal of propagules.

This study differs from similar studies in that it examines the demographic properties of two closely related species exhibiting different invasiveness, rather than comparing different populations of the same species with varying invasiveness.

Table 4.5 suggests a range of demographic properties that may differ between plants exhibiting different degrees of invasiveness.

Table 4.5 Proposed demographic differences between species with differing degrees of invasiveness.

Demographic attribute	More invasive	Less invasive
Fruit set rate	Higher	Lower
Fruit crop	Larger	Smaller
Seedling survival	Higher	Lower
Maturation time to reproduction	Shorter	Longer
Seed predation	Lower	Higher
Growth rate	Faster	Slower
Population growth	Faster ($\lambda>1$)	Slower ($\lambda\rightarrow1$)

The role of any one demographic property in determining invasiveness is equivocal, as exemplified by two shrubs invading habitats in eastern Australia. *Chrysanthemoides monilifera* (Boneseed) is non-invasive in its native habitat in South Africa, but has much higher fruit and seed output in Australia where it is invasive (Weiss and Milton 1984). This suggests the importance of escape from seed predators in newly invaded environments. However *Cytisus scoparius* (Scotch Broom) has similar seedbank densities in both its native Europe and some locations in Australia where it is non-invasive, as well as in a very invasive population on Barrington Tops, New South Wales (Smith and Harlen 1991).

4.1.7 Determination of life-table data

Central to population modelling is the formulation of life-table data. Plants, especially shrubs, present particular cases that require careful assessment of a number of components in order to adequately address the main demographic transitions. This is covered in detail in sections 4.1.8-4.1.10.

The transition matrices and data from which they are derived are specific to the 1.2 ha plot ASF1 located in the Armidale State Forest. This provides a direct comparison between *C.monogyna* and *P.mahaleb*. It was necessary for some components of the data to be derived from supplementary plots located in ASF and also at the Saleyards site. Where this data is used it is discussed in the relevant section.

4.1.8 Calculation of survival rates

Survival of *C.monogyna* and *P.mahaleb* plants was monitored over a three year period (1987-1990). The three year survival rate was then converted to an average yearly rate by taking the cube root. To illustrate, after three years, 23 individuals out of an initial population of 100 survived. This represents a three year survival rate of 0.2300 and gives rise to an average annual survival rate of $0.2300^{1/3} = 0.6127$. In other words after three years the survival of an individual would be 0.6127 x 0.6127 x 0.6127 = 0.2300.

4.1.9 Calculation of fecundity rates

Enright and Watson (1991) reiterated the point made by Caswell (1989) that many studies which model woody plant populations have seeds as the first size class. In the matrix multiplication this introduces an unnecessary time step in the transition between seed dispersal and germination. Enright and Watson (1991) and Caswell (1989) suggested that a better approach was to have a seedling class as the first class. In the case of *C.monogyna* germination begins at the end of the winter fruiting season and *P.mahaleb* begins germination approximately 6-8 months after dispersal. Although seed may experience periods of dormancy (Flemion 1938, Ellis *et al.* 1985), using seedlings rather than seeds as the first size class is unlikely to affect the models derived in this project adversely. As a consequence fecundity values in the transition matrices are expressed as seedlings per tree per year rather than seeds per tree per year.

The removal of the seed class by alternatively expressing fecundity in terms of seedlings produced per plant per year, removes the necessity of inclusion of elements in the transition matrices which relate to vegetative reproduction as there is no longer a distinction between vegetatively and sexually reproduced seedlings. This is not regarded as a disadvantage as vegetative reproduction is on the whole difficult to determine and recognize in the field (Harper

1977). Within the study plots there were very few plants that could confidently be regarded as the result of vegetative propagation. This simplification of both life-tables and transition matrices is warranted in the case of *C.monogyna* and *P.mahaleb* in this study where vegetative reproduction is very minimal. However situations may arise in the future or in other locations where vegetative reproduction is more pronounced and therefore may warrant inclusion in some form within transition matrices.

Estimation of fecundity remains a difficult task (Harper 1977). This is often the case in organisms that have 'pulse' births and continuous growth, as is the case with many trees and shrubs (Caswell 1989). Shrubs and trees are often difficult subjects as some species may be masting species where seed output varies greatly from year to year (Ogden 1985).

Another compounding factor in this study is that newly emerging seedlings of *C.monogyna*, and especially *P.mahaleb*, are very difficult to determine in the absence of cotyledons, which fall within three months of seedling emergence. This hinders accurate assessment of the fates of seedlings as they age. This is compounded in *P.mahaleb* which has seedling densities in excess of 500 seedlings m^2 (see section 4.3.3).

Given the difficulty of reliably assessing fates of newly emerged seedlings, estimation of fecundity for each species was made by comparing average annual fruit production for the whole ASF1 plot (calculated from class estimates of fruit crops, sections 4.2.2 and 4.3.2), with the total number of established seedlings in ASF1 (calculated from estimates of seedling densities, sections 4.2.3 and 4.3.3). This ratio gives an estimate of 'per-fruit' contribution to reproduction (Caswell 1989). This per-fruit figure is multiplied by the average fruit crop for each size class to yield a size class contribution to reproduction. The size class contribution to fecundity was divided by the initial size class distribution of individuals (ISD in tables 4.10, 4.11, 4.18, 4.19). This is then divided by the modal age of seedlings to give a yearly estimate of fecundity in terms of seedlings (Enright and Ogden 1979). There is no data concerning the life expectancy of seedlings, which is likely to be longer than modal age.

Enright and Ogden (1979) utilized a similar approach for the estimation of fecundity of the masting *Nothofagus fusca* (red beech). In this species "the established seedling population is more or less suppressed on the forest floor, is numerically much more stable and constitutes the 'pool' from which canopy trees are recruited and to which they must contribute for successful reproduction" (Enright and Ogden 1979, 10). *P.mahaleb* behaves in a similar fashion to *N.fusca* in that the majority of *P.mahaleb* seedlings remain suppressed under parental plants and provide recruits to the rest of the population. *C.monogyna* also has suppressed seedlings (through herbivory and overshading) which also provide recruits to the rest of the population.

Enright and Ogden (1979) did not attempt to estimate fecundities of different size classes. By expressing fecundities of *C.monogyna* and *P.mahaleb* in proportion to average fruit crops for each size class, a picture of differential fecundity emerges which is hopefully more representative of the populations under investigation.

4.1.10 Growth and transition rates

In order to estimate transition rates of individuals from one size class to the next, an estimate of the average rates of growth of individuals in each size class was made. This average growth rate was determined each year for the entire census period. This data set comprised all individuals in all plots so as to generate a conservative estimate of growth rates based on as many components of the population as possible.

The average growth rates for individuals in each size class were compared to initial size of all plants measured in ASF1 in 1987. An estimate was made for each individual as to whether, based on average growth rates, it would move into the next size class after one year (see Burns and Ogden 1985). The number of individuals passing into the next size class was expressed as a proportion of the total number of plants in the initial size class. It was hoped, by increasing the sample to include all plants measured and not relying on a small subsample to calculate transition rates, that the transitions would be conservative and avoid bias arising from factors affecting any one single plot or from sampling a few, especially vigorous plants as encountered by Burns and Ogden (1985) in their study of *Avicennia marina* in New Zealand.

4.1.11 Determination of the latent root of transition matrices

Iterative multiplication of population and transition matrices produces a stable stage distribution (SSD) in which the proportion of individuals in each size class becomes constant. This is a characteristic of matrix models where transition probabilities remain constant through time (Caswell 1989, Begon and Mortimer 1986). The rate of population change from one time period to the next also becomes stable. In order to calculate the rate of population change, the statistical package MINITAB (version 7.2, MINITAB inc., 1989) was used to post-multiply the transition matrix A by the population matrix n for each species. This process, referred to as the power method (Caswell 1989, Enright and Watson 1991) proceeded through a minimum of 100 iterations until the population matrix became stable. The rate of population growth (equal to lambda λ) was calculated by dividing the number of individuals in each size class of the n generation by the number of individuals in each class of the n-1 generation (Caswell 1989, Enright and Watson 1991).

4.1.12 Census plots for *Crataegus monogyna* and *Prunus mahaleb*

Data for survival, growth and fecundity of *C.monogyna* were collected from three large plots. One plot, ASF1 comprising

1.2 ha, was located in ASF. The other two, Saleyards 1 (1100 m^2) and Saleyards 2 (225 m^2) were located at the Saleyards site. In total 863 plants were tagged and measured in 1987.

Data for *P.mahaleb* was collected from three plots in ASF. The first plot ASF1 was the same used for *C.monogyna*. The two remaining plots, ASF2 and ASF3, each 10 m^2, were primarily used for the monitoring of seedlings located in *P.mahaleb* thickets.

In addition to the 5 main plots, up to eight 25 m^2 plots and ten 1 m^2 plots, located adjacent to ASF1, and six 1 m^2 plots adjacent to Saleyards 1 and Saleyards 2 were used to census seedlings. All 25 m^2 plots were located under the canopies of *P.radiata* and eucalypt trees in ASF, while the 1 m^2 plots were positioned under the canopies of large *P.mahaleb* trees.

The size classes for larger *C.monogyna* and *P.mahaleb* plants were defined in two ways, by height of tallest stem and by basal stem circumference. The height classes were 0-100 cm, 100.1-200cm, 200.1-300 cm, 300.1-400 cm, 400.1-500 cm and >500 cm. The 0-100 cm class consisted of non-reproductive seedlings. Basal stem circumference classes were 0-5 cm, 5.1-10 cm, 10.1-15cm, 15.1-20 cm, 20.1-25 cm, 25.1-30 cm, 30.1-35 cm and >35 cm. Basal stem circumference was used in preference to basal cross-sectional area of stem to define size classes because it was better related to fruit production and hence fecundity. See sections 4.2.2. (table 4.7) and 4.3.2. (table

4.15) for details of regression analyses of fruit crops against size of shrubs.

4.2 *Crataegus monogyna* demography

This section details information concerning flowering and the age structure of *C.monogyna* at ASF and covers the estimation of fecundity, survival and transition rates for inclusion in population matrix models.

4.2.1 Flowering success of *Crataegus monogyna*

In 1987, 1245 flowers on tagged branches on eight plants at the Saleyards site were counted to monitor fruit set rates (defined as the flower to fruit ratio by Milton and Dean (1988)). A total of 492 fruit were set on the same branches to give an average fruit set rate of 39.5%. In further investigations in 1989, 3462 flowers were counted on 28 tagged branches from three different size classes of plants. These size classes were based on height: large > 500 cm, medium 200-500 cm, and small < 200 cm. All but one plant was located within either the ASF or Saleyards sites. One isolated large shrub was located on 'Newholme', the University of New England research station, located approximately 10 km north of Armidale (see fig. 5.3). On this isolated plant 1005 flowers on 6 branches were counted. Fruit set rates ranged from 2.8% on the isolated Newholme plant to 56.7% in the smallest size class. Table 4.6 shows the fruit set rates for *C.monogyna* at the ASF, Saleyards and Newholme sites.

Table 4.6. Fruit set rates for *C.monogyna* in ASF, Saleyards and Newholme sites for Spring 1988. Numbers in brackets refer to the number of branches in each size class surveyed.

	ASF and Saleyards				Newholme			
Size class	flowers	fruit set	failed	% fruit set	flowers	fruit set	failed	% fruit set
<200cm	248(5)	141	107	56.7				
200-500cm	1589(11)	670	919	42.3				
>500cm	620(6)	257	363	41.5	1005(6)	28	977	2.8
Total	2457(22)	1068	1389	43.5	1005(6)	28	977	2.8

4.2.2 Fruit crop size of *Crataegus monogyna*

An estimate of fruit production was made by counting fruit on selected plants in different size classes at both ASF and the Saleyards sites. Fruit crops were estimated by direct counts for plants with small (< 200 fruit) fruit crops. For shrubs with large fruit crops (>200 fruit), 100 fruit were counted along a branch to provide an estimate of the number of fruit per unit volume. This unit volume was then used to estimate the entire fruit crop contained in the canopy. This method allowed rapid estimation of fruit crops to be made for many plants.

Estimated fruit crops were regressed against height of tallest stem, basal stem circumference and basal cross-sectional area of stem. Table 4.7 shows the regression equations and associated R^2 values for fruit crop estimates for 1988 and 1989.

Table 4.7 Regression equations for fruit crop estimates of *C.monogyna* at ASF in 1988 and 1989. Circumference = basal circumference (cm), height = height of tallest stem (cm), and basal area = basal cross-sectional area (cm^2), d.f. = degrees of freedom, and p = probability that ß does not equal 0.

Year	Equation	R^2(%)	d.f.	p
1988				
	Fruit = 9.7 + 18.7(circumference)	32.0	125	<0.01
	Fruit = -190 + 1.8(height)	15.5	125	<0.01
	Fruit = 246 + 3.3(basal area)	24.2	125	<0.01
	LogFruit = 4.35 + 0.053(circumference)	40.6	125	<0.01
	LogFruit = 3.3 + 0.007(height)	32.9	125	<0.01
	LogFruit = 5.06 + 0.0086(basal area)	26.0	125	<0.01
1989				
	Fruit = -2.13 + 1.4(circumference)	53.4	160	<0.01
	Fruit = -22.0 + 0.18(height)	8.1	160	<0.01
	Fruit = 19.8 + 0.037(basal area)	48.9	160	<0.01
	LogFruit = 3.39 + 0.0069(circumference)	16.1	54	<0.01
	LogFruit = 3.29 + 0.0093(height)	0.8	54	<1.0
	LogFruit = 3.58 + 0.00016(basal area)	13.7	54	<0.01

Despite considerable, yet unexpected (McCarthy and Quinn 1989) variation in the proportion of fruit explained by each variable, fruit crops were, on the whole, more closely related to basal circumference and tree height than basal cross-sectional area. For this reason the formulation of size classes for matrix population models used height of plant and basal circumference to delineate size classes (see section 4.1.12). Caswell (1989) suggested using state variables that were meaningfully related with vital rates. In this case height and basal circumference were related to fruit production. However predicted fruit crops using the equations in table 4.7 yielded unrealistically large values for fruit crops in the larger size classes. For this reason average fruit crops calculated independently for each size class were used for analyses (see table 4.8).

There is a great deal of variation in fruit crops. Coefficients of variation range from 80% up to 513%. This results from considerable differences in fruiting effort for individuals plants from one year to the next. Not all plants fruit in any one year. Compared to predicted fruit crops using regression equations the estimated fruit crops in table 4.8 can be regarded as conservative.

Table 4.8 Average fruit crops (1988 and 1989 combined) for *C.monogyna* at ASF based on height and basal circumference size classes. N = number of individual plants in each size class. Numbers are rounded to the nearest whole number.

Size class (cm)	mean number of fruit	Standard deviation	N
Seedlings			
0-100	0	-	-
Height			
100.1-200	20	57	76
200.1-300	177	284	89
300.1-400	269	452	82
400.1-500	314	373	28
>500	311	478	10
Basal circumference			
0-5	12	62	43
5.1-10	53	74	57
10.1-15	121	221	59
15.1-20	186	195	38
20.1-25	285	334	19
25.1-30	245	196	19
30.1-35	601	821	16
>35	352	480	36

4.2.3 Estimate of density, standing crop and age of seedlings.

Seedlings were defined as all plants 0-100 cm tall (see section 4.2.5). Newly emerged seedlings were recognized by having one or both dicotyledons. Plants that had lost their dicotyledons were referred to as established seedlings.

Seven 25 m^2 quadrats, located adjacent to ASF1 and under the canopies of *P.radiata* and eucalypt trees were used to estimate the density, survival and growth of *C.monogyna* seedlings. The number of seedlings found in each quadrat in 1987 were 45, 10, 6, 1, 2, 3, and 1. Densities ranged from 1.80 m^{-2} to 0.04 m^{-2} with an average density of 0.39 seedlings m^{-2} (68 seedlings in 175 m^2). This density was multiplied by the area of ASF1 (120 000 m^2) to give a total of 4680 seedlings in ASF1. This figure is used for the initial size class distribution in tables 4.10 and 4.11 in section 4.2.9.

A random sample of 150 seedlings from outside the permanent quadrats was made to determine their age. Two methods were used in unison. These were counting of annual growth rings (see section 3.1.3) and counting of bud scars (Harper 1977). Neither method was entirely satisfactory due to the small size of seedlings. Only 96 seedlings could be confidently aged. The mean age was 9.8 years with a modal age of 11 years (N = 17). Modal age was used in the calculation of fecundity because it is representative of a larger number of seedlings and is less influenced by very young or very old suppressed seedlings than is mean age.

4.2.4 Fecundity of *Crataegus monogyna*

The calculation of fecundity follows the method outlined in section 4.1.9. Tables 4.10 and 4.11 show the estimation of fecundity for each class based on average fruit crop size for each size class and an initial population of 4680 seedlings. The total fruit production is the sum of the product of rows a and f. 4680 seedlings is divided by the total fruit crop (4680/30890 = 0.152 seedlings fruit^{-1} in table 4.10; 4680/27794 = 0.168 seedlings fruit^{-1} in table 4.11). This figure is then multiplied by the average fruit per tree (row f in tables 4.10 and 4.11) for each class, and then divided by 11, the modal age of seedlings. Fecundities are rounded down to the nearest whole number. Fecundity ranged from 0-4 seedlings per tree per year for the height classes and 0-9 seedlings per tree per year in the basal-circumference classes.

4.2.5 Survival and growth of established seedlings

This class contained all plants 0-100 cm tall. The fates of seedlings were observed in the Saleyards 1 and Saleyards 2 plots, plus an additional six 1 m^2 quadrats adjacent to Saleyards 1 and Saleyards 2, and seven 25 m^2 quadrats at ASF located under *P.radiata* and eucalypt trees. Of a total of 312 seedlings (68 at ASF and 244 at the Saleyards) located on a 10 cm grid in each quadrat and measured in 1987, 253 were still alive in 1990. This gave a three year survival rate of 0.8109 or an average yearly survival rate of 0.9325. Average growth rates of seedlings from the three years of census data appear in Table 4.9.

4.2.6 Survival and growth of reproductive plants

All individuals > 100 cm tall contained in Saleyards 1 and Saleyards 2 and ASF1 were mapped, tagged with an individually numbered aluminium tag and measured for basal circumference and height of longest stem. The first census was conducted in May 1987 and each plot recensused in the winters of 1988, 1989, and 1990.

Table 4.9 Average growth rates and proportion of individuals in each size class moving up a size class for *C.monogyna* at Armidale. s.d. = standard deviation rounded to nearest whole number for height classes and one decimal place for basal circumference classes.

Size class (cm)	growth rate ($cm\ yr^{-1}$) mean (s.d.)	number of individuals in initial population	number of individuals growing into next class	proportion moving into next class
Seedlings				
0-100	7.8(7)	312	9	0.0228
height				
100.1-200	19.5(24)	128	18	0.1406
200.1-300	9.4(25)	91	10	0.1099
300.1-400	9.9(18)	87	30	0.3448
400.1-500	15(215)	112	54	0.4821
Basal circumference				
0-5	0.7(1.3)	173	18	0.1040
5.1-10	0.7(1.5)	99	15	0.1515
10.1-15	0.7(1.8)	79	19	0.2405
15.1-20	1.1(1.7)	49	14	0.2857
20.1-25	2.5(2.0)	26	11	0.4231
25.1-30	2.2(2.1)	29	11	0.3793
30.1-35	1.1(1.5)	14	4	0.2857

The rate of growth of plants was calculated for each 100 cm size class from the difference in height from year to year (see table 4.9). These average rates of growth from each of the three years were used to estimate the number of individuals in each size class in the initial population likely to grow into the next largest size class. This figure expressed as a proportion of the initial size class was the transition rate used for the construction of transition matrices (TRU in tables 4.10 for height classes and 4.11 for basal circumference classes).

4.2.7 Age structure of *Crataegus monogyna*

In 1991, a sample of 46 plants from Saleyards 1 and Saleyards 2 and 121 plants in ASF1 were felled by chainsaw and the age of plants estimated from counting of annual growth rings (for details of preparation of samples see section 3.1.3). Age revealed by ring counts was regressed against height and basal circumference of each plant. The regression equation

$$\text{Age} = 8.12 + (0.351 \times \text{basal circumference in cm}) \quad (12)$$

($R^2 = 64.2\%$, $N = 167$, $P<0.01$) was used to predict the age of the remaining 64 individuals not felled in ASF1.

The number of plants that fell into each yearly age class was expressed as a proportion of the total number of plants in ASF1. Figure 4.1a shows the age structure of *C.monogyna*.

C.monogyna is characterized by an expanding population with a fairly constant rate of recruitment. This pattern is similar to that reported by van der Maarel, Boot, van Dorp and Rijntjes (1985) for *C.monogyna* in the Netherlands. Like the situation here, there was a dominance of trees in the mid-aged classes suggesting that population growth may occur from dispersal of propagules from numerous loci (van der Maarel, Boot, van Dorp and Rijntjes 1985) rather than a population dominated by one or a few old individuals which are the source of all younger plants.

4.2.8 Causes of morbidity and mortality of *Crataegus monogyna*

Losses to the population through death occur throughout all components of the population. Predation of fruit occurs both on the tree and ground (see chapter 5 for discussion of avian seed predators). Some ground predation of seeds by vertebrates probably occurs. Fallen fruit is likely to be ingested occasionally by ground foraging dispersers (foxes, macropods) and not killed (see also Chapter 5).

A simple assessment of seed removal form seed depots was undertaken to gauge the level of possible seed predation. During a two week period in 1989 (last week in August and first week of September) 150 seeds in 15 depots each with ten seeds were laid out along two parallel 12 m transects in ASF1 but > 5 m from the nearest fruiting *C.monogyna* plant. Only 3 seeds were removed, presumed predated. If predation remained constant over the entire year this would equate to a yearly predation rate of 52% (78/150).

Some invertebrates also predate *C.monogyna* seeds. Removal of the stony endocarp sometimes revealed a grub in the seed cavity with either no seed or a severely damaged seed. Although not apparently common, invertebrate seed predation may still warrant further investigation, particularly if biological control of *C.monogyna* ever becomes an issue.

The effect of seed predation on the population is probably minimal in comparison to losses to the population through death of seedlings. Newly emerged seedlings tended to suffer from desiccation in mid- to late-summer. Grazing by cattle, sheep and rabbits was also likely to account for some seedling mortality. This was more pronounced at the Saleyards site which was consistently and more heavily grazed by sheep and cattle. Outside the plots, a large number of seedlings were killed after they were covered by a large cow pad (cattle faeces). Williams and Buxton (1986) also reported a similar occurrence of death by defecation. This is unlikely to be a common cause of death for the majority of seedlings as many seedlings occur on rocky ground which is largely avoided by stock.

Seedlings growing in deep shade under *C.monogyna* thickets almost always died. Larger seedlings, especially on the edges of thickets, appeared to have better chances of survival. In well established thickets some individuals were likely to encounter high rates of intraspecific competition either for water, nutrients or light. Tall spindly individuals with sparse foliage characterized by high mortality rates provide an indication of the intensity of competition. Recruitment in thickets is likely to be by coppice growth or following death of large shrubs which may open up the canopy, releasing suppressed seedlings.

Away from thickets survival of individuals was enhanced by rocks and fallen timber which provided protection from grazing. Some plants were very stunted with relatively large girths and did not flower or produce fruit. Cessation of grazing by sheep and cattle would probably allow these plants to grow rapidly above browsing height and consequently reach larger reproductive size classes (see Williams and Buxton 1986 for similar fates of *C.monogyna* in New Zealand after cessation of grazing). A significant reduction in rabbits may also lead to accelerated growth by reduction in grazing pressure (van der Maarel, Boot, van Dorp and Rijntjes 1985).

Many adult plants were infested with a cherry slug which fed on the leaf lamina. The appearance of browning foliage towards the end of summer suggested that some trees were severely affected. However there were no deaths attributed to cherry slug herbivory. It is possible that defoliation may have affected fruit production of some individual plants but this was not assessed. The degree of attack was variable between trees, and between years. Estimation of fruit crops was made after leaf fall in winter. Consequently the effect of insect defoliation on fruit production was not assessed.

The response to damage of *C.monogyna* varied in relation to the size of plants. Seedlings were usually killed while larger plants responded by vigorous regrowth. After felling of trees by chainsaw in 1991 in preparation for determination of plant age, most large shrubs resprouted from their cut stumps. This has implications for control of *C.monogyna* if plants are removed by felling. There is a need to follow cutting with application of systemic herbicides to the freshly cut stump.

4.2.9 Life-tables and transition matrices for *Crataegus monogyna*

Table 4.10 shows the life-table data for *C.monogyna* grouped into height classes. Growth rates were fastest for the 100.1-200 cm class. No mortality was recorded for the larger size classes. The survival rate of 1 must be an overestimate and suggests that an even longer census period is warranted. Fecundity is concentrated in the 200.1-400 cm size range with individuals in this size range contributing >70% of estimated fecundity. Many of the taller plants >500 cm have proportionately more dead and dying limbs and consequently smaller fruit crops than would be expected, compared to more vigorous smaller plants.

Table 4.11 shows the life-table data for plants allocated into basal circumference classes. Fecundity is concentrated in the two largest size classes, accounting for nearly half the reproductive output of the population at ASF.

The division of *C.monogyna* into basal circumference classes (table 4.11) yielded more classes than the height classes used. The matrix based on height classes (table 4.12) had a larger latent root of 1.13804 and therefore faster rate of projected population growth compared to the matrix based on basal circumference classes (table 4.13) with a latent root of 1.10293.

Table 4.10 Initial size class distribution, growth rates, survival rates, transition probabilities and fecundity for *C.monogyna* near Armidale. Size classes based on height of tallest stem.

	Size classes height (cm)					
	0-100	100.1-200	200.1-300	300.1-400	400.1-500	>500
a ISD	4680	61	52	47	16	9
b GR	7.8(7)	19.5(2)	9.4(25)	9.9(18)	15(215)	-
c SR	0.9325	0.9848	0.9769	1	1	1
d TRU	0.0288	0.1406	0.1099	0.3448	0.4821	-
e TRS	0.9712	0.8594	0.8901	0.6552	0.5179	1
f Fruit/tree	0	20	177	269	314	311
g TFSC	0	1220	9204	12643	5024	2799
h Fecundity	0	0	2	3	4	4

ISD: initial size-class distribution of individuals at the 1.2 ha ASF site. GR: average growth rate (cm yr^{-1}) for each size class, standard deviation appears in brackets. SR: survival rate of individuals (yr^{-1}). TRU: proportion of individuals moving to the next size class. TRS: proportion of individuals staying in the same size class. TFSC: Total number of fruit produced by each size class (row a x row f). Fecundity expressed as seedlings produced per tree per year and rounded down to the nearest whole number (4680 divided by sum of row g (30 890 fruit) multiplied by row f (fruit per tree in each size class) and divided by modal age of seedlings (11 years). See also section 4.2.4 for explanation of calculation of fecundity.

Table 4.11 Initial size class distribution, growth rates, survival rates, transition probabilities and fecundity for *Crataegus monogyna* at Armidale. Size classes based on height of plants 0-100 cm, and basal circumference for plants > 100 cm tall.

	Size classes height (cm)	basal circumference (cm)							
	0-100	0-5	5.1-10	10.1-15	15.1-20	20.1-25	25.1-30	30.1-35	>35
a ISD	4680	30	42	44	24	8	13	6	18
b GR	7.8(7)	0.7(1.3)	0.7(1.5)	0.7(1.8)	1.0(1.7)	2.5(2.0)	2.2(2.1)	1.1(1.5)	2.7(71)
c SR	0.9325	0.9672	0.9952	0.9866	1	1	0.9901	1	0.9895
d TRU	0.0288	0.1040	0.1515	0.2405	0.2857	0.4231	0.3793	0.2857	-
e TRS	0.9712	0.8960	0.8485	0.7595	0.7143	0.5769	0.6207	0.7143	1
f Fruit/tree	0	12	53	121	186	285	246	601	352
g TFSC	0	360	2226	5324	4464	2280	3198	3606	6336
h Fecundity	0	0	0	1	2	4	3	9	5

ISD: initial size-class distribution of individuals at the 1.2 ha ASF site. GR: average growth rate (cm yr^{-1}) for each size class, standard deviation appears in brackets. SR: survival rate of individuals (yr^{-1}). TRU: proportion of individuals moving to the next size class. TRS: proportion of individuals staying in the same size class. TFSC: Total number of fruit produced by each size class (row a x row f). Fecundity expressed as seedlings produced per tree per year and rounded down to the nearest whole number (4680 divided by sum of row g (27 794 fruit) multiplied by row f (fruit per tree in each size class) and divided by modal age of seedlings (11 years). See also section 4.2.4 for explanation of calculation of fecundity.

Table 4.12 Transition matrix for *Crataegus monogyna* at Armidale. Size classes are based on height of tallest stem. Data from table 4.10. See explanation in text (section 4.1.5) for calculation of matrix elements. λ=1.13804.

Size classes height (cm)	0-100	100.1-200	200.1-300	300.1-400	400.1-500	>500
0-100	0.9055	0	2	3	4	4
100.1-200	0.0269	0.8463	0	0	0	0
200.1-300	0	0.1385	0.8695	0	0	0
300.1-400	0	0	0.1074	0.6552	0	0
400.1-500	0	0	0	0.3448	0.5179	0
>500	0	0	0	0	0.4821	1

Table 4.13 Transition matrix for *Crataegus monogyna* at Armidale. Size classes are based on height for plants 0-100 cm tall and basal circumferences for plants > 100 cm tall. Data from table 4.11. See explanation in text (section 4.1.5) for calculation of matrix elements. λ=1.10293.

	Size classes height (cm)	basal circumference (cm)							
	0-100	0-5	5.1-10	10.1-15	15.1-20	20.1-25	25.1-30	30.1-35	>35
0-100	0.9055	0	0	1	2	4	3	9	5
0-5	0.0269	0.8666	0	0	0	0	0	0	0
5.1-10	0	0.1006	0.8444	0	0	0	0	0	0
10.1-15	0	0	0.1515	0.7493	0	0	0	0	0
15.1-20	0	0	0	0.2373	0.7143	0	0	0	0
20.1-25	0	0	0	0	0.2857	0.5769	0	0	0
25.1-30	0	0	0	0	0	0.4231	0.6146	0	0
30.1-35	0	0	0	0	0	0	0.3755	0.7143	0
>35	0	0	0	0	0	0	0	0.2857	0.9895

4.3 *Prunus mahaleb* demography

This section deals primarily with the estimation of fecundity, survival and transition elements for inclusion in population matrix models. This section also addresses flowering success and age structure of *P.mahaleb* populations at ASF. All analyses and methods are the same as those used for *C.monogyna* except where specified.

4.3.1 Flowering success in *Prunus mahaleb*

In 1987, 1295 flowers were counted tagged branches on 10 plants at ASF. From these flowers 269 fruit were borne at an average fruit set rate of 20.8%. In 1988 a similar procedure to that used for *C.monogyna* was followed to monitor fruit set rates in different sized plants (table 4.14). 4061 flowers on 40 tagged branches were counted. Fruit set rates ranged from 6.2% (17 fruit from 276 flowers) in the largest size class to 18.5% (90 fruit from 486 flowers) in the 200-500 cm class. Average fruit set rates were 10.5% in plants located in the main *P.mahaleb* population. Isolated plants on the edges of the population had lower fruit set rates which averaged 5.0%.

Table 4.14 Fruit set rates for *P.mahaleb* in isolated and non-isolated plants, Spring 1988. Numbers in brackets refer to the number of branches in each size class surveyed.

	Non-isolated				Isolated			
Height size class (cm)	flowers	fruit set	failed	% fruit set	flowers	fruit set	failed	% fruit set
<200cm	1478(10)	129	1349	8.7	28(2)	1	27	3.6
200.1-500cm	486(8)	90	396	18.5	425(5)	8	417	1.9
>500cm	276(5)	17	259	6.2	1368(10)	83	1285	6.1
Total	2240(23)	236	2004	10.5	1821(17)	91	1730	5.0

4.3.2 Fruit crop size in *Prunus mahaleb*

An estimate of fruit production was made by counting fruit on selected branches on individuals from different sized plants at ASF. Fruit were estimated by direct counts for plants with small crops (< 200 fruit) and estimated for plants with larger crops as outlined in section 4.2.2. Fruit crop estimates are based on an average of two years' data.

As encountered with *C.monogyna* fruit crops, the prediction of *P.mahaleb* fruit crops using the regression equations in table 4.15 significantly overestimated crops, especially for the larger size classes. Again, for the purposes of the construction of matrices, a more conservative estimate based on average fruit crops for each 100 cm size class was used (see section 4.2.2). Table 4.16 shows the average fruit crop for each size class. Maximum fruit production occurred in the largest size class. Only a few individuals produced in excess of 10,000 fruit. Most trees had crops of fewer than 5000 fruits. This may be more of a function of the age of the population of *P.mahaleb* at ASF. As the population ages the average production of fruit per tree might be expected to increase.

Table 4.15 Regression equations for fruit crop estimates of *P.mahaleb* at ASF in 1988 and 1989. Circumference = basal circumference (cm), height = height of tallest stem (cm), and basal area = basal cross-sectional area (cm^2).

Year	Equation	R^2(%)	d.f.	p
1988				
	Fruit = 79 + 7.9(circumference)	5.4	17	<0.5
	Fruit = -787 + 4.0(height)	32.1	17	<0.05
	Fruit = 167+ 2.2(basal area)	4.7	17	<0.5
	LogFruit = 0.92 + 0.012(circumference)	52.8	14	<0.01
	LogFruit = 3.3 + 0.007(height)	20.8	14	<0.1
	LogFruit = 5.06 + 0.0086(basal area)	32.8	14	<0.05
1989				
	Fruit = -499 + 68.0(circumference)	53.3	117	<0.01
	Fruit = -1629.0 + 9.45(height)	45.5	117	<0.01
	Fruit = 254 + 8.84(basal area)	45.9	118	<0.01
	LogFruit = 3.29 + 0.072(circumference)	62.3	76	<0.01
	LogFruit = 1.1 + 0.013(height)	73.2	76	<1.0
	LogFruit = 4.54 + 0.0067(basal area)	32.5	77	<0.01

These fruit crop estimates for *P.mahaleb* overlap with the range of fruit production reported by Herrera and Jordano (1981) where estimated total crops ranged from 2400 fruit for trees *c.* 300-350 cm tall to 80 000 fruit for an individual 450 cm tall; 50 cm tall or smaller plants did not produce fruit.

Table 4.16 Average fruit crops (1988-1989) for *P.mahaleb* at ASF based on height and basal circumference size classes.

Size class (cm)	mean number of fruit	Standard deviation	N
height			
0-100	0	-	
100.1-200	22	58	59
200.1-300	86	118	33
300.1-400	950	1071	17
400.1-500	1708	2183	12
>500	5267	4096	12
basal circumference			
0-5	2	3.8	33
5.1-10	28	52	35
10.1-15	175	360	17
15.1-20	170	155	11
20.1-25	283	202	3
25.1-30	1150	1277	4
30.1-35	1000	796	7
>35	3563	3673	24

4.3.3 Estimation of density, standing crop and age of seedlings.

In contrast to *C.monogyna*, a large number of seedlings germinate and survive under the canopies of large trees (generally >550 cm tall and with basal circumference 50 cm). These trees, hereafter referred to as nursery trees, must offer suitable conditions for seed germination, and protection from desiccation of newly emerged seedlings compared to exposed dispersed seedlings. Fifteen nursery trees were identified in ASF1. All were large and all produced large fruit crops > 5000 fruit.

The pattern of seedlings under the canopies of these nursery trees resembled an annulus, with a few or no seedlings immediately around the base of the main trunk surrounded by a 'halo' of very dense seedlings. A estimate of the number of seedlings under nursery trees was calculated by estimating the combined area of annuli and multiplying this by the average density of seedlings under nursery trees.

The average area of annuli was estimated by using the formula

$$A = 3.14 \times (r_1^2 - r_2^2) \qquad (13)$$

where r_1 and r_2 are the mean radii of the seedling free area and extremity of the seedling halo respectively. r_1 and r_2 were measured for 12 of the 15 nursery trees with mean values of 3.96 m and 1.39 m respectively. The combined area of annuli was calculated as 645 m^2.

The density of seedlings under nursery trees was estimated from four 0.5 m x 0.5 m quadrats placed randomly in seedling halos. Measured seedling densities were 816, 772, 692 and 676 seedlings m^{-2} giving a mean density of 739 seedlings m^{-2}. Seedling densities were also estimated away from nursery trees. Six 25 m^2 quadrats located under *P.radiata* canopies had seedling densities of 0.60, 1.88, 0.44, 1.08, 1.44 and 1.72 seedlings m^{-2}, which gave a mean of 1.2 seedlings m^{-2}.

The standing seedling crop in ASF1 was calculated as (645 m^2 x 739 seedlings m^{-2}) + (11355 m^2 x 1.2 seedlings m^{-2}), which gave an initial standing crop of 490 281 seedlings.

An estimation of the age of seedlings was made from a random sample of 150 seedlings harvested from the outer third of the seedling halo under the canopy of a nursery tree located adjacent to ASF1. Age was determined by a combination of counting of annual growth rings and annual bud scars (see section 4.2.3). This was very difficult due to the very small size of seedlings, and only 83 seedlings were confidently aged. The 83 seedlings had mean and modal ages of 5.8 ± 3.1 and 8 years respectively.

4.3.4 Fecundity of *Prunus mahaleb*

The calculation of fecundity follows the method outlined in section 4.1.9. Tables 4.18 and 4.19 show the estimation of fecundity for each class based on average fruit crop size for each size class and an initial population of 490281 seedlings. The total fruit production is the sum of the product of rows a and f. 490281 seedlings is divided by the total fruit crop (490281/276879 = 1.770 seedlings $fruit^{-1}$ in table 4.18; 490281/166639 = 2.942 seedlings $fruit^{-1}$ in table 4.19). This figure is then multiplied by the average fruit/tree (row f in tables 4.18 and 4.19) for each class, and then divided by 8, the modal age of seedlings. Fecundities are rounded down to the nearest whole number.

4.3.5 Survival and growth of established seedlings.

In addition to plants in the two 10 m^2 plots in ASF, all plants 0-100 cm tall in six 1 m^2 located under *P.radiata* trees and four 0.25 m^2 quadrats under *P.mahaleb* nursery trees were used to monitor survival and growth of prereproductive plants.

Of 576 seedlings recorded in 1987, 470 survived after three years to give a three year survival rate of 0.8160 and an average yearly survival of 0.9345. The growth rate and transition probabilities for *P.mahaleb* seedlings are shown in table 4.17.

Table 4.17 Average growth rates and proportion of individuals in each size class moving up a size class for *P.mahaleb* at Armidale. s.d. = standard deviation rounded to the nearest whole number for height and one decimal place for basal circumference classes.

Size class (cm)	growth rate ($cm\ yr^{-1}$) mean (s.d.)	number of individuals in initial population	number of individuals growing into next class	proportion moving into next class
Seedlings				
0-100	7.5(7.0)	182	9	0.0495
height				
100.1-200	15.7(23)	207	26	0.1256
200.1-300	14.0(28)	46	7	0.1522
300.1-400	19.5(27)	9	1	0.1111
400.1-500	19.5(27)	5	3	0.6000
Basal circumference				
0-5	0.6(1.0)	362	42	0.1160
5.1-10	0.9(1.8)	54	12	0.2222
10.1-15	1.5(2.1)	25	9	0.3600
15.1-20	1.8(3.5)	13	4	0.3077
20.1-25	2.3(2.8)	11	4	0.3636
25.1-30	2.7(3.5)	14	8	0.5714
30.1-35	2.3(2.6)	8	3	0.3750

4.3.6 Survival and growth of reproductive plants.

All individuals >100 cm tall in ASF1 were located, measured for basal circumference and height of longest stem, and tagged with individually numbered aluminium tags in May 1987. This procedure was repeated in ASF2 and ASF3, each 10 m^2, located within a *P.mahaleb* thicket. A total of 1260 plants were censused in 1987. The plants located in the 1.2 ha plot formed the basis of the matrix modelling and provided the initial size class distribution in table 4.21 and 4.19. The plots were recensused in the winters of 1988, 1989 and 1990.

The proportion of individuals in each class surviving and moving into other size classes was estimated over the three year period. Average growth rates were calculated from the three years of census data. By comparing the average growth rates with the initial population in 1987 an estimate of the number of individuals in each size class that would be likely to move into the next size class was expressed in proportion to the initial population. Table 4.17 summarizes the average annual growth rates and the proportion of each size class moving into the next class.

4.3.7 Age structure of *Prunus mahaleb*

The same methods outlined in section 4.2.7 were used for the determination of the age structure of *P.mahaleb*. Age of individual plants estimated from counting annual growth rings

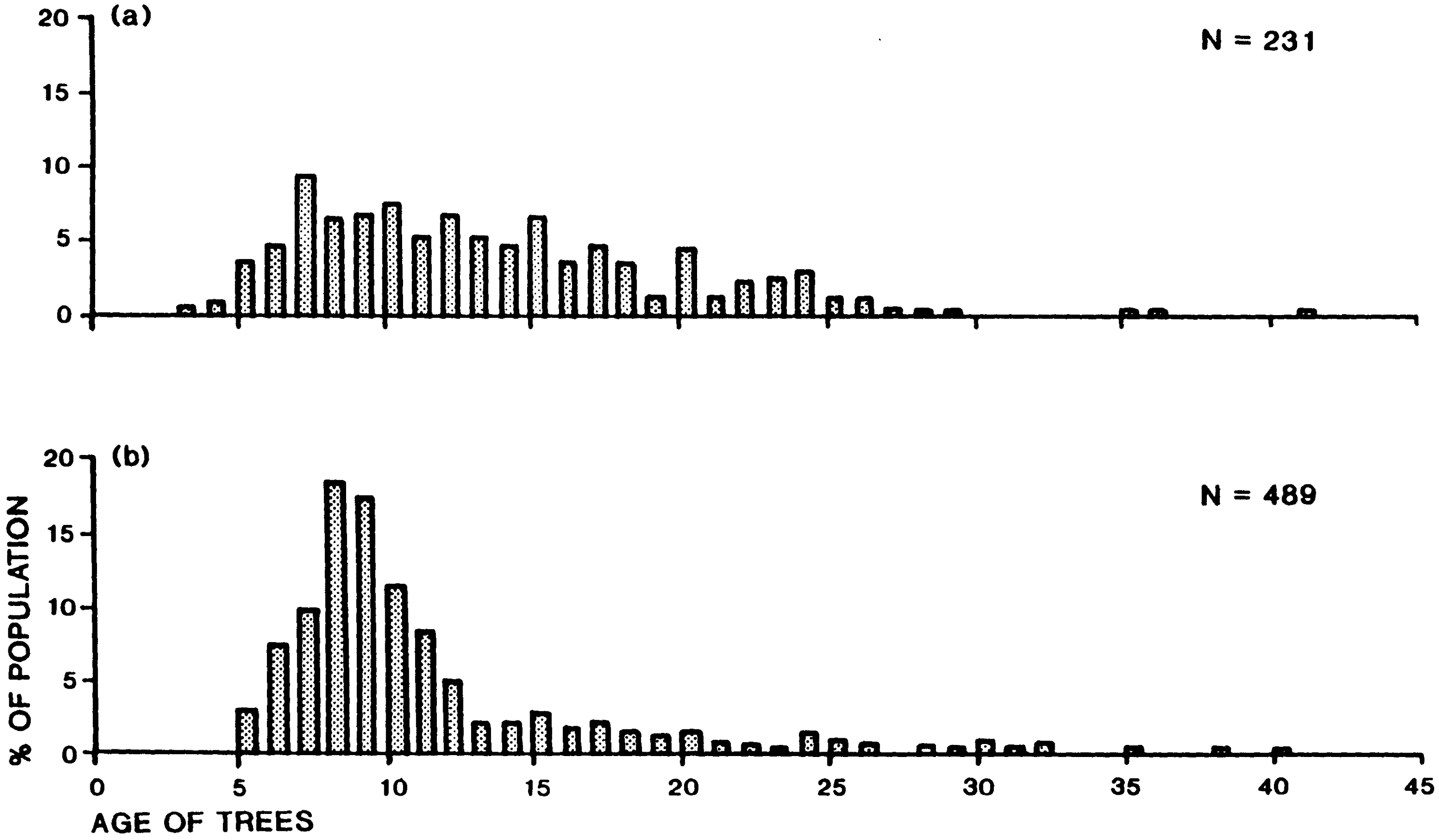

Figure 4.1 Age structure of (a) *C.monogyna* and (b) *P.mahaleb* in ASF1 estimated from trees > 1 m tall felled in 1991.

was regressed against basal stem circumference. The regression equation

$$\text{Age} = 7.21 + (0.276 \times \text{basal circumference in cm}) \quad (13)$$

(R^2 = 79.6%, N= 346) was used to predict the ages of a further 143 plants not felled in the 1.2 ha plot.

Figure 4.1b shows the age structure of *P.mahaleb* at ASF. Approximately 50% of all plants in ASF1 were less than 10 years of age at the time of felling in 1991. This structure is characteristic of an expanding population. Only plants > 1 m tall were felled. Therefore no young plants were collected and this left an apparent 'gap' in the age structure in Fig. 4.1b.

4.3.8 Causes of mortality in *Prunus mahaleb*

Mortality occurs at every stage of the life cycle of *P.mahaleb*. The duration of this project precluded assessment of factors which may operate on older plants. However some assessment of morbidity suggest that disease and boring insects endemic in stone fruit trees may also affect *P.mahaleb*. Three mid-sized individuals exuded resin from small active (expelled wood dust was deposited around the entrance to the hole) insect(?) bore holes. These trees remained alive during the duration of the census period but produced noticeably small fruit crops. Feral fruit trees may be an important refuge for pest organisms and disease which may allow reinfection of commercial fruit crops in orchard growing regions.

Death of individuals was most common in the small size classes, including seeds. Variation in seed and seedling mortality appears to be related to density and proximity to parental plants. The extremely high seed and seedling densities under parent, and in particular nursery, trees promote a range of fates for progeny.

Two sets of experiments were conducted to examine the difference in predation between seeds dispersed away from (>2 m) trees and those located under parent trees over a two week period in February immediately after all *P.mahaleb* fruit had disappeared from fruiting trees. To simulate dispersed seeds, 170 seeds were placed in 17 depots of 10 seeds each, with 2 m between each depot along two parallel transects of 16 m and 14 m in ASF1 under *P.radiata* trees in 1988. After two weeks nine seeds were removed, and presumed predated. This was repeated in mid-January 1989 with a total of 150 seeds in 15 depots. In this instance seeds were left checked weekly until no further seeds had been removed after two consecutive weeks. Of 100 seeds only 9 seeds had been removed after 7 weeks (16/1/1989-6/3/1989).

A further 100 seeds in 10 depots of 10 seeds each were placed under the canopy of a nursery tree in 1988. After two weeks 57 seeds had been removed, presumed predated. Although not conclusive this simple experiment suggests that seeds located under parent trees experience much higher rates of seed predation (probably by mice or rats) than do seeds dispersed away from fruiting trees, a phenomena shared by other *Prunus* species (Webb and Willson 1985). This is largely expected as seed predation may be influenced by density dependent factors (Harper 1977). This high rate of predation under parent trees must be weighed against any possible benefits through satiation of predators (Louda 1989). Large concentrations of seeds under parents may attract predators there rather than to dispersed seeds which may consequently escape predation.

This pattern of seed mortality has to considered in the light of seedling survival. Nursery trees must provide suitable conditions for seed germination and the establishment of seedlings, as evidenced by the very high seedling densities experienced there. Conversely conditions away from nursery trees are less favourable. Seedlings apparently experience higher insolation and desiccation away from nursery trees. The main cause of death amongst seedlings was moisture stress experienced in the height of summer.

Cattle, rabbits and possibly kangaroos browse on leaves and shoots of *P.mahaleb*. There was evidence of damage by grazing to plants in the smaller size classes (<300 cm tall). In the largest individuals browse damage was confined to the lower branches. There was significant grazing damaged seen in seedlings.

The response to felling of plants by chainsaw was similar to that of *C.monogyna*. *P.mahaleb* plants once felled resprouted. However where there was a large suppressed seedling crop under large trees, especially nursery trees, there was vigorous and rapid growth of seedlings. This has important implications for the control of *P.mahaleb* if clear-felling is involved. A suitable herbicide application or repeated felling must take place before plants reach reproductive maturity.

4.3.9 Life-tables and transition matrices for *Prunus mahaleb*

Tables 4.18 and 4.19 summarize the growth, survival, fecundity and transition data for *P.mahaleb* classes by height and basal circumference respectively. The highest fecundity occurs in the largest size classes. As with *C.monogyna* no mortality was recorded in the largest classes leading to a survival rate of 1, an obvious overestimation. A longer census period may have revealed a more realistic estimation of mortality in the larger size classes.

Table 4.18 Initial size class distribution, growth rate, survival rates, transition rates and fecundity for *Prunus mahaleb* at Armidale. Size classes are based on height of tallest stem. Numbers in brackets relate to fecundity rates incorporating 13626 seedlings dispersed away from nursery trees.

	Size classes height (cm)					
	0-100	100.1-200	200.1-300	300.1-400	400.1-500	>500
a ISD	490281	117	34	17	23	41
b GR	7.5(7.0)	15.7(23)	14.0(2.9)	19.5(27)	19.5(27)	19.5(27)
c SR	0.9345	0.9815	1	1	1	1
d TRU	0.0495	0.1256	0.1522	0.1111	0.6000	-
e TRS	0.9505	0.8744	0.8478	0.8889	0.4000	1
f Fruit/tree	0	22	86	950	1708	5267
g TFSC	0	2574	2924	16150	39284	215947
h Fecundity	0	4	19	210	377	1165
	(0)	(0)	(0)	(5)	(10)	(32)

ISD: initial size-class distribution of individuals at the 1.2 ha ASF site. GR: average growth rate (cm yr^{-1}) for each size class, standard deviation appears in brackets. SR: Survival rate of individuals (yr^{-1}). TRU: proportion of individuals moving to the next size class. TRS: proportion of individuals staying in the same size class. TFSC: total number of fruit produced by each size class (row a x row f). Fecundity expressed as seedlings produced per tree per year and rounded down to the nearest whole number (490281 divided by the sum of row g (276879), multiplied by row f (fruit per tree in each size class) and divided by modal age of seedlings (8 years). See also section 4.2.4 for explanation of calculation of fecundity.

Table 4.19 Initial size class distribution, growth rates, survival rates, transition rates and fecundity for *Prunus mahaleb* at Armidale. Size classes are based on height for plants 0-100 cm tall and basal circumference for plants > 100 cm tall. Numbers in brackets relate to fecundity rates incorporating 13626 seedlings dispersed away from nursery trees.

Size classes	height (cm)	basal circumference (cm)							
	0-100	0-5	5-10	10-15	15-20	20-25	25-30	30-35	>35
a ISD	490281	79	45	26	14	9	13	9	37
b GR	7.5(7.0)	0.6(1.0)	0.9(1.8)	1.5(2.1)	1.8(3.5)	2.3(2.8)	2.7(3.5)	2.3(2.6)	3.4(5.8)
c SR	0.9345	0.9742	0.9791	0.9615	1	1	1	1	1
d TRU	0.0495	0.1160	0.2222	0.3600	0.3077	0.3636	0.5714	0.3750	-
e TRS	0.9505	0.8840	0.7778	0.6400	0.6923	0.6364	0.4286	0.6250	1
f Fruit	0	2	28	175	170	283	1150	1000	3562
g TFSC	0	158	1260	4550	2380	2547	14950	9000	131794
h Fecundity	0	0	10	64	62	104	422	367	1309
	(0)	(0)	(0)	(1)	(1)	(2)	(11)	(10)	(36)

ISD: initial size-class distribution of individuals at the 1.2 ha ASF site. GR: average growth rate (cm yr^{-1}) for each size class, standard deviation appears in brackets. SR: survival rate of individuals (yr^{-1}). TRU: proportion of individuals moving to the next size class. TRS: proportion of individuals staying in the same size class. TFSC: total number of fruit produced by each size class (row a x row f). Fecundity expressed as seedlings produced per tree per year and rounded down to the nearest whole number (490281 divided by the sum of row g (166639), multiplied by row f (fruit per tree in each size class) and divided by modal age of seedlings (8 years). See also section 4.2.4 for explanation of calculation of fecundity.

Table 4.20 Transition matrix for *Prunus mahaleb* at Armidale. Size classes are based on height of tallest stem. Numbers in brackets refer to fecundity rates based on seedlings dispersed away from nursery trees. λ = 1.71346. (For seedlings dispersed away from nursery trees λ = 1.22431).

Size classes height (cm)	0-100	100.1-200	200.1-300	300.1-400	400.1-500	>500
0-100	0.8882	4	19	210	377	1165
		(0)	(0)	(5)	(10)	(32)
100.1-200	0.0463	0.8582	0	0	0	0
200.1-300	0	0.1233	0.8478	0	0	0
300.1-400	0	0	0.1522	0.8889	0	0
400.1-500	0	0	0	0.1111	0.4000	0
>500	0	0	0	0	0.6000	1

Table 4.21 Transition matrix for *Prunus mahaleb* at Armidale. Size classes are based on height of tallest stem for plants < 100 cm tall and basal circumference in cm for plants > 100 cm tall. Numbers in brackets refer to fecundity rates based on seedlings dispersed away from nursery trees. λ = 1.49409 (For seedlings dispersed away from nursery trees λ = 1.18559).

	Size classes height (cm)	Basal circumference (cm)							
	0-100	0-5	5.1-10	10.1-15	15.1-20	20.1-25	25.1-30	30.1-35	>35
0-100	0.8882	0 (0)	10 (0)	64 (1)	62 (1)	104 (2)	422 (11)	367 (10)	1309 (36)
0-5	0.0463	0.8612	0	0	0	0	0	0	0
5-10	0	0.1130	0.7615	0	0	0	0	0	0
10-15	0	0	0.2176	0.6154	0	0	0	0	0
15-20	0	0	0	0.3461	0.6923	0	0	0	0
20-25	0	0	0	0	0.3077	0.6364	0	0	0
25-30	0	0	0	0	0	0.3636	0.4286	0	0
30-35	0	0	0	0	0	0	0.5714	0.6250	0
>35	0	0	0	0	0	0	0	0.3750	1

4.4 Discussion of the demographies of *C.monogyna* and *P.mahaleb* at Armidale

Fruit set rates were generally much higher for *C.monogyna* at 43.5% than *P.mahaleb* at 10.5%, although in both cases plants that were isolated from the main concentration of each population had much lower fruit set rates. The reason behind the differences between *C.monogyna* and *P.mahaleb* is unclear. Reduced fruit set rates has implications for invasion. Limited genetic variation within a species due to poor fruit set may be detrimental to a species success and physiological plasticity in a new invaded environment which may have a bearing on invasiveness.

Fruit crops are generally larger in *P.mahaleb* than *C.monogyna* (tables 4.8 and 4.17) especially in the larger size classes where there is an order of magnitude difference. These differences are carried through to fecundity in terms of seedlings produced per tree per year. *P.mahaleb* maintains an order of magnitude greater fecundity in the largest size classes (tables 4.13 and 4.23; and tables 4.14 and 4.24).

Seed predation rates are higher for *P.mahaleb* seeds located under parent plants than those dispersed away from parent plants. *C.monogyna* seed predation rates were consistently lower than that recorded for *P.mahaleb*. One factor important here is density related. The local concentration of *P.mahaleb* seeds in ASF, especially under fruiting plants, is such that it provides a powerful attractant to seed predators which can readily find seeds with little effort. On the other hand *C.monogyna* seeds are comparatively rare in ASF and occur in a diffuse pattern. Predation of *P.mahaleb* seeds is likely to be intense and to a certain extent systematic while for *C.monogyna* it is likely to be relatively infrequent and accidental. Seedling recruitment in both species is enhanced by the proximity of fallen branches, logs, low overhanging branches and rocky ground which all offer some protection from grazing (Morgan 1991).

Manipulation of matrix elements to gauge the sensitivity of matrix models to errors (see tables 6.1-6.4 in chapter 6) suggests that even major errors or reduction in fecundity are unlikely to greatly affect projected population growth rates. A reduction in fecundity of 50% for both species produced relatively small reductions in projected growth rates. As a consequence errors in the estimation of fecundity are unlikely to dramatically effect the results obtained by matrix modelling of the populations.

Some difficulties arise from the measurement of basal circumferences of both *C.monogyna* and *P.mahaleb*. Both species grew on rocky and uneven ground. Some plants had prominent boles or basal swellings which may have arisen from a number of factors including genetic variability and suppression by periodic grazing. This resulted in some variation in the measurement of individuals from year to year. This variation was overcome to a certain extent by ensuring that basal circumference measurements were taken as close to the ground and around the widest point. The use of field assistants while I was on crutches may have introduced some further variation in techniques although all helpers were thoroughly briefed as to how measurements were to be made with the aim of reducing such errors.

P.mahaleb has slightly faster growth rates than *C.monogyna*, which extends through to calculation of transition rates (tables 4.9 and 4.17). The rates of growth for *C.monogyna* at Armidale for height (7-19.5 cm yr^{-1}) fall in the range of values derived by Williams and Buxton (1986) in New Zealand (10-31 cm yr^{-1}).

Survival rates are similar for both species. However the overestimation of survival for the larger size plants suggests that a longer census period is needed for both species. It seems likely that the population of both species are too young at present to include plants old enough to become senescent, and to die through other accidental causes.

The latent roots of the transition matrices are on the whole lower for *C.monogyna* than *P.mahaleb*. For analyses based on height classes *C.monogyna* has a λ = 1.13804 (table 4.12) and *P.mahaleb* has λ = 1.71346-1.22431 (table 4.20). For analyses based on basal circumferences the roots are *C.monogyna* λ = 1.10293 (table 4.13) and *P.mahaleb* λ = 1.49409-1.18559 (table 4.21).

The occurrence of suppressed seedlings beneath parent trees is not restricted to *P.mahaleb*. *Prunus serotina*, a close relative has suppressed seedlings up to 60 years of age (Auclair and Cottam 1971) which respond with vigorous growth to canopy openings (Smith 1975). The majority of *P.mahaleb* seedlings occur under nursery trees and contribute greatly to the projected population growth. The much higher fecundity levels shown for *P.mahaleb* resulted mainly from inclusion of a large number of non-dispersed seedlings located under nursery trees, and this leads to the high projected population growth rate. If only the much smaller number of dispersed seedlings are considered, this results in a much lower fecundity rate, and leads to a projected population growth rate which only marginally exceeds that calculated for *C.monogyna.*

This picture of higher rates of population growth of *P.mahaleb* compared to *C.monogyna* is reinforced by looking at the age structure of both populations. *P.mahaleb* is characterized by a relatively young population dominated by individuals about 10 years old. On the other hand *C.monogyna* has a less skewed population. van der Maarel, Boot, van Dorp and Rijntjes (1985) also found a similar pattern in *C.monogyna* in the Netherlands. He suggested that this was a function of reproduction in the *C.monogyna* population being the result of individuals from many foci entering the population as dispersed seeds rather than reproduction being concentrated on a few individuals. If this was the case at ASF it should be borne out by investigation of the seed dispersal systems of both species.

Despite *C.monogyna* having a slower rate of projected population growth than *P.mahaleb,* it still maintains higher relative invasiveness as measured by rate of spread (Chapter 3). The apparent inconsistency with expected demographic behaviour (see table 4.5, section 4.1.6) perhaps adds more weight to the suggestions of Mack (1985) (section 3.1, Fig. 3.1) that rate of spread and hence invasiveness may be related to increased numbers of infection foci. Likewise the establishment of effective dispersal systems (Noble 1989, Bazzaz 1986) may ensure a higher degree of invasiveness for *C.monogyna* than *P.mahaleb.* It is this aspect that is dealt with in detail in the next chapter.

CHAPTER 5: DISPERSAL ECOLOGIES OF CRATAEGUS MONOGYNA AND PRUNUS MAHALEB

The importance of dispersal of propagules as an integral part of range expansion of plants is well recognized (Birks 1989). This is particularly so when dealing with biological invasions where extent and rate of spread are important factors (see Chapter 3) and if high population growth is to be effectively realized by invading plants (see Chapter 4). Bazzaz (1986) and Noble (1989) recognized that without effective seed dispersal systems invading plants will be unlikely to attain high rates of range expansion.

Ridley (1930) documented many examples of seed dispersal which highlighted the diverse nature of seed dispersal. This diversity of dispersal techniques, systems, strategies and interactions between plants and animals set the stage for Van der Pijl (1972) to systematically address seed dispersal, thereby clearing ambiguities in the terminology. This was accomplished principally by the introduction of new terms, some of which took on unwieldy forms. Van der Pijl (1972) did however clarify the definition of dispersal systems based largely on perceived adaptational traits of diaspores. Relevant to this thesis is that some diaspores are specifically adapted for dispersal by vertebrates, and in particular by birds. Seeds are presented in such a fashion (usually within a fruity pulp or with nutritional appendages) as to attract dispersal agents which in turn ingest seeds in order to obtain nourishment from the fruit pulp or appendage. Many authors have since expanded the discussion of seed dispersal systems to address within-syndrome variation. The results of endozoochory (seed transport inside vertebrate guts) in achieving potentially spectacular dispersal distances (Proctor 1968) vary in quality and quantity from one dispersal agent to another (Herrera and Jordano 1981, Reid 1989).

5.1 Specialist and generalist dispersal systems

Two types of dispersal systems involving birds are widely recognized (Snow 1981). The first is a specialist syndrome characterized by plants that produce a few highly nutritious fruit and rely on one or a few largely or solely frugivorous animals to act as dispersal agents. This system results in a high degree of fidelity of the dispersal agent for the plant. This is commonly found in tropical areas where intense competition between plants for dispersers has led to the development of coevolved specialist dispersal systems. On the other hand generalist syndromes tend to involve plants that produce large amounts of nutritionally poor fruit that are available to a wide range of dispersers (Howe and Smallwood 1982, Snow 1981). These very broad generalization have been weakened by successive studies which have moved from tight coevolution (Mckey 1975) to diffuse coevolution (Herrera 1982) prompted by discovery of variability in dispersal systems. This is particularly so where sets of complex relationships exist between fruit size, fruit and seed predation, disperser behaviour and climate and is especially evident in multispecies assemblages e.g. Herrera (1984). The inherent variability in dispersal systems has confounded attempts to seek a general explanation for the development of seed dispersal systems. Sallabanks and Courtney (1993) however regard variability seen in seed dispersal systems as the result of selection by plants to parallel the variability shown in the behaviour of dispersers, which is again a response to environmental variability. This view may help explain the large degree of variability which has defeated the search for an all encompassing generalization concerning dispersal systems.

5.2 Biological invasions and seed dispersal

To describe the invasiveness of a species, it is necessary to measure the areal extent of the population and the rate at which it expands its range (Roughgarden 1986). Range expansion is ultimately facilitated by seed dispersal (Bazzaz 1986, Noble 1989), by which a propagule reaches a safe site for germination (*sensu* Harper 1977) and subsequent establishment. Both long- and short-distance dispersal overcomes some of the barriers that are characteristic of invasions through stable windows (see section 1.1.8, Johnstone 1986). With specific relevance to this project, discussion of seed dispersal will be confined to vertebrate dispersal of seeds contained in the fruit of introduced woody plants in temperate Australia.

Mulvaney (1986), Buchanan (1978, 1989), Bass (1989, 1990) and other authors have looked at vertebrate seed dispersal of introduced ornamental garden plants in south eastern Australia, many of which are now regarded as invasive weeds. Birds, especially Pied Currawongs *Strepera graculina*, have been implicated as major dispersal agents involved in woody weed invasions in the region. The role of both native and introduced mammals as dispersal agents of introduced plants has however been largely neglected but may be important in local range expansion of some introduced species (Bass 1990).

The rate at which an introduced plant expands its range will be greatly affected by the "quality" and "quantity" of seed dispersal. Quality of dispersal relates to the arrival of seeds in safe sites (Harper 1977). This may express itself as dispersal away from density dependent mortality factors such as predators (Janzen 1970, Howe and Smallwood 1982), pathogens (Ridley 1930) and parental and sibling competition (Harper 1977). Quantity relates specifically to the number of seeds dispersed from a parent plant and is a function of the capacity of a dispersal agent to remove seeds, which in turn relates to an animal's physiology and behaviour before and after ingesting seeds. Species-specific factors such as animal physiology and behaviour will also affect quality of dispersal. Environmental factors such as surrounding vegetation (Debussche *et al.* 1982) may also affect where seeds will be voided. Other local factors may be important; Somerset (1975) reported on the weed flora established under a Wedge-tailed Eagle's nest, the end result of the eagles feeding on rabbits that had ingested weed seeds. The nature of substrates which receive dispersed propagules will also affect the survival of seeds and seedlings (Reid 1989).

Because seed dispersal is critical in determining the invasive potential of a plant (Bazzaz 1986, Noble 1989), intuitively, it would be expected that there would be differences in seed dispersal systems between invasive and non-invasive species. Invasive species would be expected to have highly efficient and well developed seed dispersal systems with high quality and/or quantity of fruits adapted for long-distance dispersal of their contained seeds. Non-invasive species would be characterized by poorly developed low quality and quantity dispersal systems that would suffer high rates of seed predation.

Knight (1986a,b) suggested that invasive fleshy fruiting species in South Africa have large and intense (more conspicuous) fruiting displays than native species. It may be that in general, more invasive species may have larger and more intense fruit displays than less invasive species. This relates also to the dynamic relationships between fruiting plants and potential dispersers. Invasive plants may possibly alter the frugivorous patterns in a region so that ingestion of native fruits is reduced and hence dispersal of native plants is also reduced (Knight 1986a, Debussche and Isenmann 1990).

5.2.1 Interactions between introduced fruiting plants and birds

Very few temperate zone bird species are entirely frugivorous (Barker and Vestjens 1989, 1990). Those birds having generalist diets utilizing invertebrates (as does the Pied Currawong) face food shortages during cooler months (Wimbush 1969). Seasonal shortages of natural/native food supplies for native birds and other animals will likely see a shift in food resources to relatively more available non-native food resources. The types of foods available to animals in times of low invertebrate abundance in cooler months include human refuse (composting heaps in gardens, open garbage bins, refuse dumps) and ornamental and cultivated fruiting plants. In Armidale a diverse range of introduced fruiting plants are available. These include species of *Pyracantha*, *Cotoneaster*, *Crataegus*, *Ligustrum* and *Pistacia*.

The phenomenon of altitudinal and latitudinal migrant birds congregating in urban areas is relatively widespread in temperate regions (e.g. Debussche and Isenmann (1990) in the Mediterranean, and Nakanishi (1991) in Japan). Pied Currawongs, regarded as altitudinal migrants (Wimbush 1969, Frith 1976) have been shown to congregate around towns during autumn and winter throughout New South Wales (Readshaw 1968, Wimbush 1969). A ready supply of food may increase over-winter survival of Pied Currawongs. The changes in autumn-winter migration patterns of birds in the Montpellier region in France reported by Debussche and Isenmann (1990) are possibly driven by increased availability of introduced fruit in and around towns as native fruit becomes scarce. By providing fruit as food for birds invading fleshy fruiting plants have large numbers of their seeds dispersed by birds.

From the work of Knight (1986a,b) and Debussche and Isenmann (1990), there are two components that may affect invasiveness of fleshy fruiting plants. Adaptive traits of fruit and fruit presentation may be different, and/or there may be differences in the behaviour and efficacy of the suite of dispersers. In the absence of interspecific competition any single ornamental plant may receive adequate seed dispersal. With increased competition from other introduced fruiting species for dispersers, the most visually, architecturally and nutritionally attractive fruits should receive better dispersal and hence have a greater invasive potential.

5.3 Assessment of the dispersal ecologies of *Crataegus monogyna* and *Prunus mahaleb*

The methods used here to describe the dispersal systems of *C.monogyna* were different to those used for *P.mahaleb*. The two reasons for this stem from the fact that their fruiting phenologies are different (see chapter 2). *C.monogyna* fruits in autumn and winter while *P.mahaleb* fruits in summer. Consequently the dispersal vectors are different. In addition *P.mahaleb* has a non-persistent fruit (Herrera 1989) with a short fruiting season of *c.* 1 month which is very predictable temporally and spatially. Persistence of fruit crops is defined by Herrera (1989) as characterizing those species where 90% of fruit does not fall naturally to the ground within three weeks after ripening.

On the other hand *C.monogyna* in Australia has persistent fruit (although Herrera (1989) categorizes *C.monogyna* in Europe as having non-persistent fruit) with a long fruiting season which extends over six months. This results in a diffuse fruiting season and potentially an extended period of seed dispersal, especially over a wide geographical area.

As a result of these differences in fruit between the two species, and variations in disperser behaviour, it has proved possible to assemble a wealth of data from direct observations of feeding and dispersal events for *P.mahaleb*, while there is a paucity of equivalent material for *C.monogyna*. In order to construct a picture of the dispersal system of *C.monogyna* data was collected largely by observations of dispersal vector behaviour and analysis of voided and hence dispersed material, rather than direct observations of frugivory. Identification of faecal material was made with reference to Triggs (1984).

5.3.1 The characteristics of *Crataegus monogyna* and *Prunus mahaleb* fruit.

The fruit and fruit displays of *C.monogyna* and *P.mahaleb* differ in important and significant ways. This section presents specific information on the physical and chemical characteristics relevant to disperser behaviour and is summarized in Table 5.1.

The fruit of *C.monogyna* are relatively large *c.* 1 cm in diameter, generally containing one large endocarp with seed. It has a relatively nutritious pulp which is quite pithy. On the other hand *P.mahaleb* with its high percentage of nonstructural carbohydrates (83.4 % compared with mean for other Mediterranean fruit of 67.0 %) is regarded more as a watery and sugary fruit, but also has a single large endocarp with seed. The importance of an extremely high concentration of iron in the pulp of *P.mahaleb* fruit (205 mg/kg of pulp compared with an average for Mediterranean fruit of 31.4 mg/kg) is unknown. It may impart a specific taste to the fruit which may be attractive to dispersers. The influence of geology and soils on the elemental concentrations in fruit is also unknown.

Table 5.1 The physical and biochemical characteristics of *C.monogyna* and *P.mahaleb* fruit (from Herrera 1987). Numbers in brackets are data for Armidale material collected in 1989.

Physical characteristics	*C.monogyna*		*P.mahaleb*	
colour	red-orange		black	
fruit display	non-bicoloured (may be bicoloured at very beginning and end of season)		bicoloured	
persistence	yes-6 months		no < 1 month	
fruit length (mm)	12.1	(9.40)	8.0	(9.1)
fruit width (mm)	9.3	(10.4)	8.3	(8.9)
mass fresh fruit (mg)	675.4	(575.8)	378.0	(510.0)
mass of seed (mg)	123.7	(89)	79.5	(110.0)
mean seed number	1	(1.05)	1	(1)
Chemical analysis				
% lipid	2.3		3.2	
% protein	2.5		2.8	
% fibre	20.5		5.7	
% NSC[1]	72.4		83.4	
% water content[2]	56.4		63.8	(73.4)
% ash	4.3		6.3	
Ca (g/kg)	4.4		1.0	
Mg (g/kg)	0.6		0.3	
P (g/kg)	0.5		0.4	
K (g/kg)	12.5		15.7	
Na (g/kg)	0.3		0.3	
Fe (mg/kg)	28		205	
Mn (mg/kg)	3		1	
Zn (mg/kg)	6		3	
Cu (mg/kg)	4		1	

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[1] NSC = Nonstructural carbohydrates

[2] Water content calculated for whole fruit (seed plus pulp)

5.4 *Crataegus monogyna*

5.4.1 Bird facilitated seed dispersal

As stated above, in the Armidale area the fruiting season of *C.monogyna* extends over a period of six months. This extended fruiting season combined with the widespread distribution of *C.monogyna* in the area means that the probability of recording fruit eating by animals at any one location over a short observation period is low.

This section aims to present a picture of the type of dispersal available to *C.monogyna*. The data relating to seed dispersal of *C.monogyna* is restricted to collection of dispersed seeds rather than direct observations of fruit ingestion and subsequent dispersal. The principal avian disperser in the Armidale area in winter is the Pied Currawong (*Strepera graculina*), a large omnivorous and gregarious bird and regular visitor to the city during the autumn and winter months. Most individuals leave the city area in spring, and nest in native forests elsewhere in the region. The Pied Currawong has been widely reported as a major disperser of fleshy fruiting introduced plants elsewhere in southeastern Australia (Mulvaney 1986, Buchanan 1989). The behaviour of Pied Currawongs was therefore studied to reveal behaviour that may be conducive to seed dispersal of *C.monogyna*. The fruit preferences of Pied Currawongs were also studied in order to assess the role of *C.monogyna* in their diet. This was established by analysis of regurgitated pellets collected systematically at two locations in Armidale, and opportunistically throughout the area. Stomach contents of road, cat or accidentally killed Pied Currawongs were also analysed. The relationship of Pied Currawong diets and the planted and naturalised fleshy fruiting introduced flora in Armidale was examined by estimation of the relative abundance of fleshy fruiting plants around Armidale.

From April to September 1989, 1990 and 1991, a total of 162 hours of direct observations of *C.monogyna* trees spread over a combined period of 27 days yielded no observations of birds ingesting whole fruit. These observations were undertaken with equal effort at both the Saleyards and ASF sites. These formal observations were complemented by casual observations during times when plants were censused (see chapter 4). The only birds observed feeding in *C.monogyna* were Eastern and Crimson Rosellas *Platycercus eximius* and *P.elegans*. These birds detached fruit from the tree and proceeded to crack open the seeds thereby killing them. In this way these Rosellas acted as seed predators rather than dispersers. Mulvaney (1986) also found in caged bird feeding trials that Rosellas killed seeds rather than ingesting and potentially dispersing intact seeds.

Throughout the duration of the project Pied Currawongs were often observed perching in *C.monogyna* trees. On one occasion at the Saleyards site, over 50 Pied Currawongs were counted perching in three *C.monogyna* trees for approximately 30 minutes. No fruit feeding took place. Some birds were observed foraging for invertebrates under the bark of *Angophora* *floribunda* trees and amongst pasture grasses. However later the same day and at the same location 12 regurgitated Pied Currawong pellets were recovered from under three nearby (< 5 m) *Angophora floribunda* trees, which contained an average of 12 ± 5.3 whole, and apparently undamaged *C.monogyna* seeds. This is probably an underestimate of the number of fruit capable of being ingested by Pied Currawongs as some of the pellets were obviously parts of pellets that had broken up on impact with overgrowing limbs or the ground. This provides evidence of local dispersal by Pied Currawongs of *C.monogyna* over distances < 10 m.

The birds listed in Table 5.2 may ingest fruit and disperse seeds of *C.monogyna* in the Armidale region; only Pied Currawongs were recorded dispersing *C.monogyna* in this study. Other birds have also been recorded ingesting *C.monogyna* fruit and seeds elsewhere in Australia (Barker and Vestjens 1989, 1990). Barker and Vestjens' lists also included birds that would be regarded as seed predators (for example *Platycercus eximius* and *P.elegans*).

In Armidale the birds likely to be important dispersers of *C.monogyna* are Pied Currawongs, Starlings (*Sturnus vulgaris*, introduced from Europe) and Silvereyes (*Zosterops lateralis*). These birds are common and occur in the region throughout the entire fruiting season. Blackbirds (*Turdus merula*, introduced from Europe), were relatively uncommon in the region. Occasional records of one or two Blackbirds in Armidale have been made since 1977. Only occasional individuals were seen in

Armidale in any given winter between 1988 and 1991 (J.Jenkins *pers comm.*, J. Humphreys *pers comm.*, D. Bass personal observations) and they were rarely recorded during summer.

Table 5.2 Birds ingesting *C.monogyna* fruit and dispersing seeds. Names follow Blakers *et al.* (1984).

- Muscicapidae
  - Grey shrike-thrush *Colluricincla harmonica*
  - Blackbird *Turdus merula*

- Meliphagidae
  - White plumed honeyeater *Lichenostomus pencillatus*
  - Eastern Spinebill *Acanthoryhnchus tenuirostris*

- Sturnidae
  - Common starling *Sturnus vulgaris*

- Dicaeidae
  - Mistletoebird *Dicaeum hirundinaceum*

- Zosteropidae
  - Silvereye *Zosterops lateralis*

- Corcoracidae
  - White-winged Chough *Corcorax melanorhamphos*

- Cracticidae
  - Pied Currawong *Strepera graculina*

- Corvidae
  - Australian raven *Corvus coronoides*
  - Little raven *Corvus mellori*

Late departure and early arrival of other migrant species such as Noisy Friarbirds (*Philemon corniculatus*) may provide an opportunity for seed dispersal by birds other than those mentioned above. Longmore (1991) shows a plate by G. Chapman of a Noisy Friarbird perching in a fruiting *C.monogyna* tree in Canberra. In Armidale, Noisy Friarbirds are usually present only at times when a large proportion of fruit is unripe at the onset of fruiting, and when a large proportion of fruit is desiccated at the end of the season. This would tend to detract from the attractiveness of *C.monogyna* fruit to Noisy Friarbirds and hence any role for these birds for dispersal of *C.monogyna* at Armidale is likely to be limited, even though they are important dispersers for *P.mahaleb* (see section 5.5.1).

5.4.2 Pied Currawong behaviour and seed dispersal

Pied Currawongs are very abundant in the Armidale region especially during the cooler months of autumn and winter. They characteristically congregate in large flocks and feed on the fruit of many ornamental garden and street trees. Winter flocking is associated with changing food availability (Readshaw 1968 and Wimbush 1969). In summer invertebrates form a large component of Pied Currawong diets (Buchanan 1989). With the onset of cooler weather invertebrate abundance drops and Pied Currawongs switch to fruit as their main food (Buchanan 1983,1989). The influx of Pied Currawongs into urban areas in winter has been documented by many authors (Roberts 1942, Wimbush 1969, Vellenga 1980, Strong 1966, Readshaw 1968). A similar picture of migratory birds in the Montpellier region of France was described by Debussche and Isenmann (1990). The Blackcap (*Sylvia atricapilla*) and four other species congregate in urban and or vineyard areas as native food sources are depleted, where they exploit introduced foods, especially fruit of *Pyracantha* and *Cotoneaster* species.

Figure 5.1 shows the relative abundance of Pied Currawongs in Armidale from 1988 to 1990. Relative abundance was determined from continuous records from March 1988 to September 1990 made while driving along a predetermined 6.8 km route from the south western corner of Armidale to the University of New England. All birds perching, feeding and flying were recorded up to five days weekly (Monday-Friday). Observations were made between 0730 and 0900 h. For each calendar month the total number of birds counted were totaled and divided by the total number of observation days. This gave the average number of Pied Currawongs seen per observation for each month. Days that were foggy were removed from calculations.

A major influx of Pied Currawongs into Armidale takes place around March. Highest numbers occur in April to June. By late September and October the number of Currawongs has declined markedly. This seasonal pattern is consistent with patterns of seasonal abundances reported by Readshaw (1968), Wimbush (1969) and others and is best explained by a shift in food abundances from invertebrates in the warmer months to fruit in the cooler months. With the onset of warmer weather, the need for breeding territories and increased invertebrate abundance result in migration by Pied Currawongs to more remote forested areas (Recher 1976, Frith 1976).

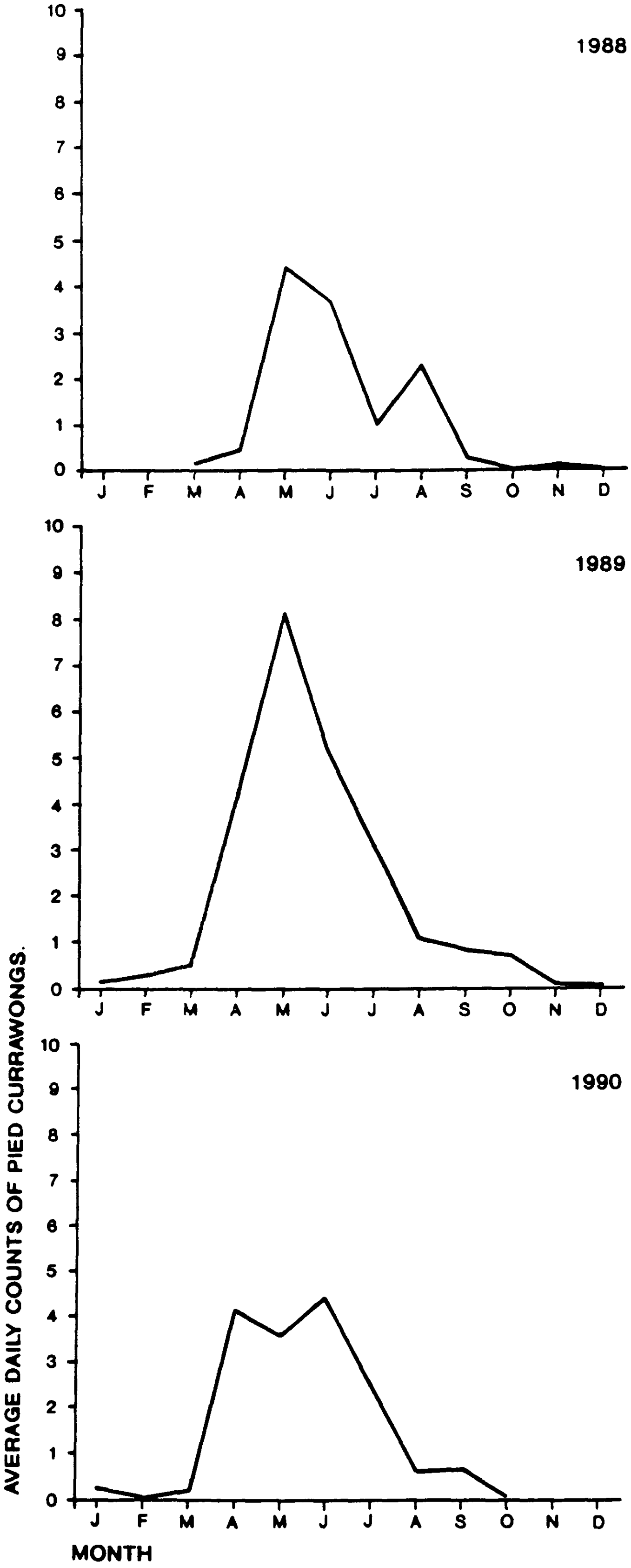

Figure 5.1 Relative abundance of Pied Currawongs in Armidale between 1988 and 1990. Data derived from daily observations along a 6.8 km transect (see text for details).

As well as a seasonal migrational pattern of Pied Currawong abundance, during the winter months there is also a diurnal pattern of bird movements. In the early morning Pied Currawongs can be seen flying into Armidale in loose flocks along more or less regular flight paths. The birds move into the city where they feed on fruit of fleshy fruiting shrubs and trees, many of which are ornamental. In the late afternoon the birds can be seen flying out of town along the same flight paths.

A number of flight paths were observed around Armidale (see Fig. 5.2). During 1988 a series of observations were made of Pied Currawongs flying along a flight path between Armidale and the Armidale State Forest north west of the township. Counts of birds flying over a location in ASF were made between 0600 and 0730 h on 31 July and 4 August 1988 and 1600 and 1730 h on 28 and 29 July and 3 August 1988. The analysis of these flights is shown in Fig. 5.3. A minimum of 249 birds on the morning of 4 August and a maximum of 509 birds in the afternoon of 29 July were recorded. On a series of afternoons birds were followed further into ASF where they congregated in an overnight roost in *Pinus radiata* trees. The distance from Armidale to the roost site in ASF was approximately 6 km. Growing under the roost were many individuals of *Ligustrum* and *Pyracantha*.

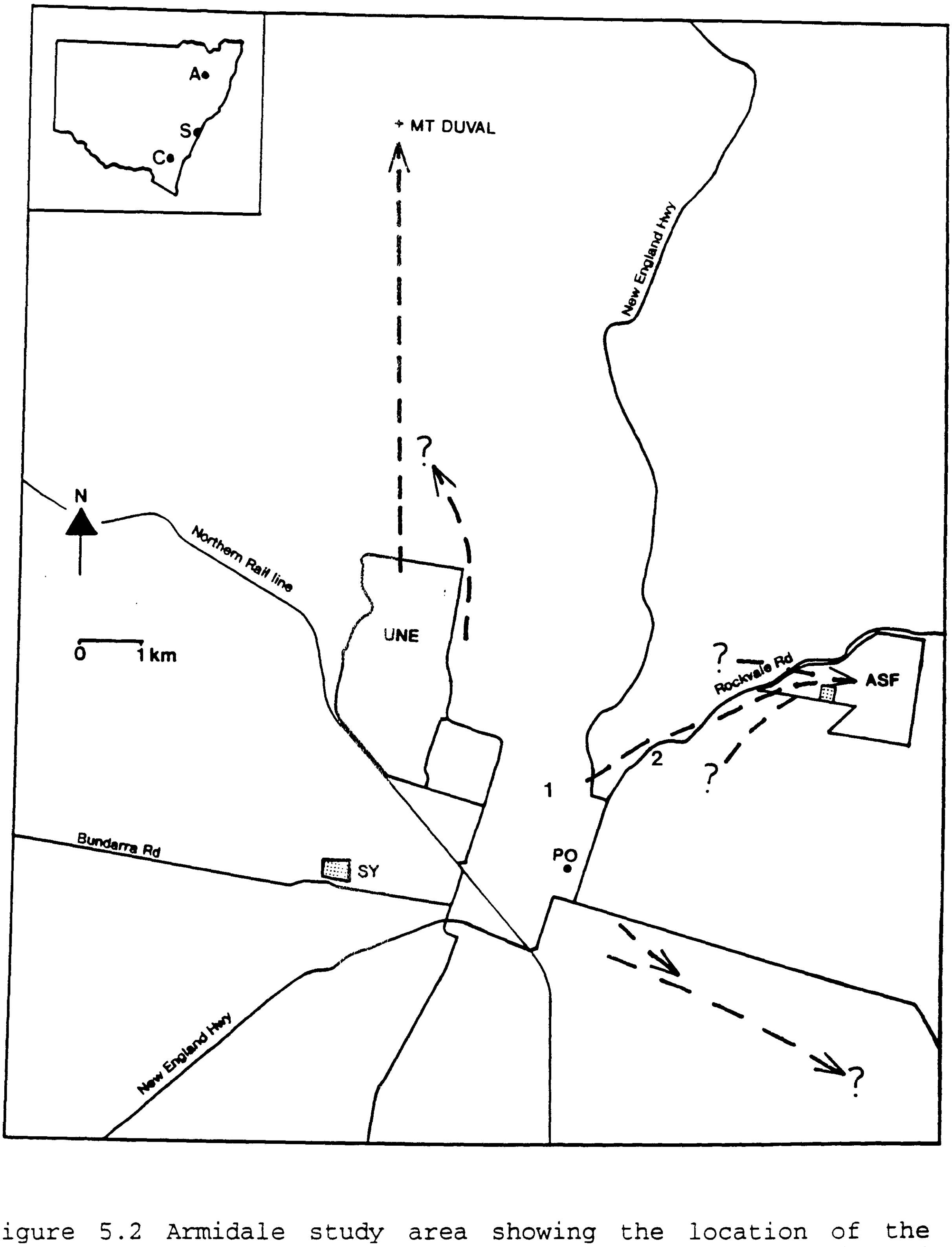

Figure 5.2 Armidale study area showing the location of the Armidale State Forest (ASF), Saleyard site (SY), University of New England (UNE), Water tower site (1) and the bird bath site (2) used for the collection of Pied Currawong ejecta. Dashed lines represent Pied Currawong flight paths out of Armidale. Inset showing New South Wales and locations of A = Armidale, S = Sydney and C = Canberra.

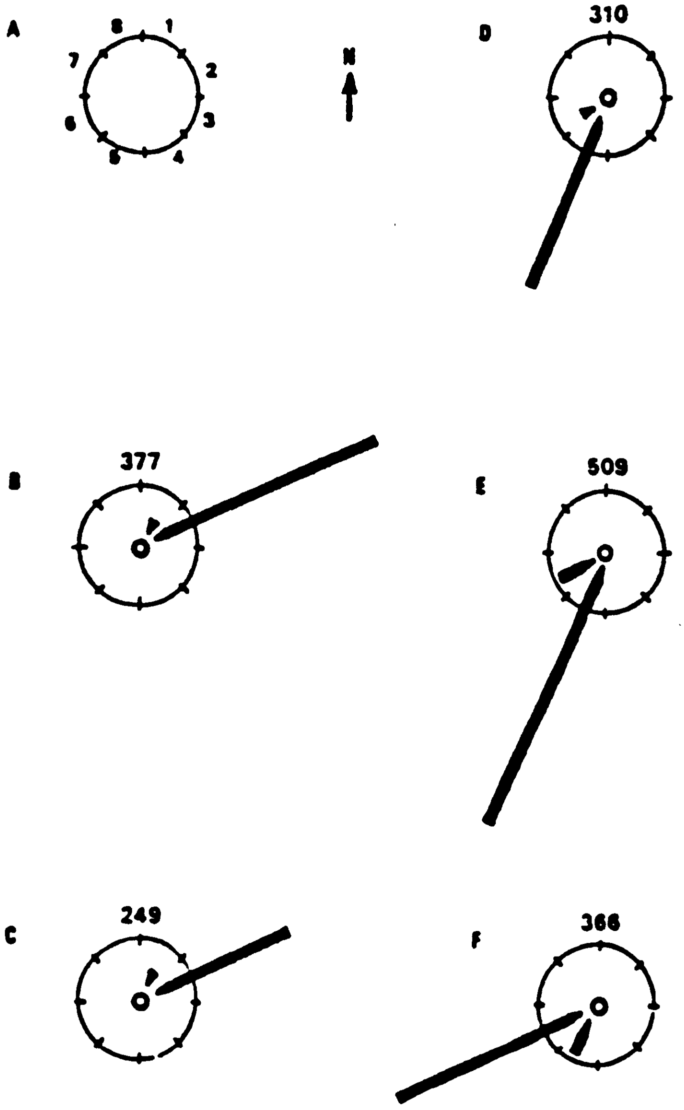

Figure 5.3 Breakdown of flight direction and numbers of Pied Currawongs observed over ASF in 1988. A shows sector numbers. B and C represent morning flights out of ASF on 31 July and 4 August respectively. D, E and F represent afternoon flights into ASF on 28, 29 July and 3 August respectively. The centre of each circle represents the observation point adjacent to ASF1. Numbers along side circles refer to the total numbers of Pied Currawongs observed in each time period and the length of the lines are proportional to the numbers of birds for each sector. (Modified from Bass 1990).

Another flight path north of the city was observed on a series of successive afternoons in 1989. With the aid of 10X binoculars, Pied Currawongs were followed in flight for a distance of approximately 9 km as they flew over the University of New England grounds towards Mt Duval (see Fig. 5.3). A large proportion (17 out of 49 birds observed) flew continuously without break until they were lost from sight on the forested slopes of Mt. Duval. A Currawong with a crop full of fruit regurgitates seeds usually on reaching a suitable perch. Therefore some of these flights to Mt Duval would be discrete seed dispersal events over long distances.

This diurnal pattern during winter coincides with fruiting of many woody plants, particularly ornamental species, and is conducive to long distance seed dispersal of fleshy fruiting woody plants facilitating their range expansion away from their points of introduction. This may lead to an expanding halo of plants around towns as seeds are dispersed into the surrounding countryside, such as has been observed in the region along a road transect described by Smith (1985). Dispersal of *C.monogyna* seeds by cars, although possible (Wace 1977) is probably rare near Armidale.

5.4.3 Pied Currawong autumn-winter diets in Armidale

An assessment of the winter diets of Currawongs was undertaken during 1989. This was accomplished by collection of regurgitated pellets from two sites in north Armidale (see Fig. 5.2). One site was a water tower on North Hill forming part of the water supply system for the township of Armidale. Pied Currawongs flew to the top of the water tower and often regurgitated pellets there. The pellets either fell to the ground or were dislodged by wind or rain and accumulated on a concrete apron around the base of the tower. Pellets were collected by sweeping the apron every week. The second collecting site was a bird bath located on a residential property on the Rockvale Road on the north east outskirts of the city. The bird bath, with a diameter of 0.5 m, was located under a *Eucalyptus viminalis* tree. Pied Currawongs perched in the tree and used the bird bath as a source of drinking water. The bird bath accumulated regurgitated pellets and was cleaned weekly.

The total number of seeds collected from each site was totaled for each week. The most common seeds collected were *Pyracantha* spp and *Ligustrum lucidum*. By the nature of the two sites the water tower had a larger number of regurgitated seeds, and range of species (N = 20, see Fig. 5.4) however this site did not maintain tight control on temporal patterns. Some pellets may have remained on the water tower roof for many weeks before being washed off as evidenced by a weathered *P.cerasifera* seed found in mid-winter whereas fruit of this species should be available only in summer. The bird bath yielded fewer species (N = 16, see Fig. 5.5) but better represented temporal patterns of fruit availability and consumption by Pied Currawongs. *Pyracantha* was the most prevalent fruit during April and May. By the end of May *L.lucidum* was the most common fruit recovered. This pattern

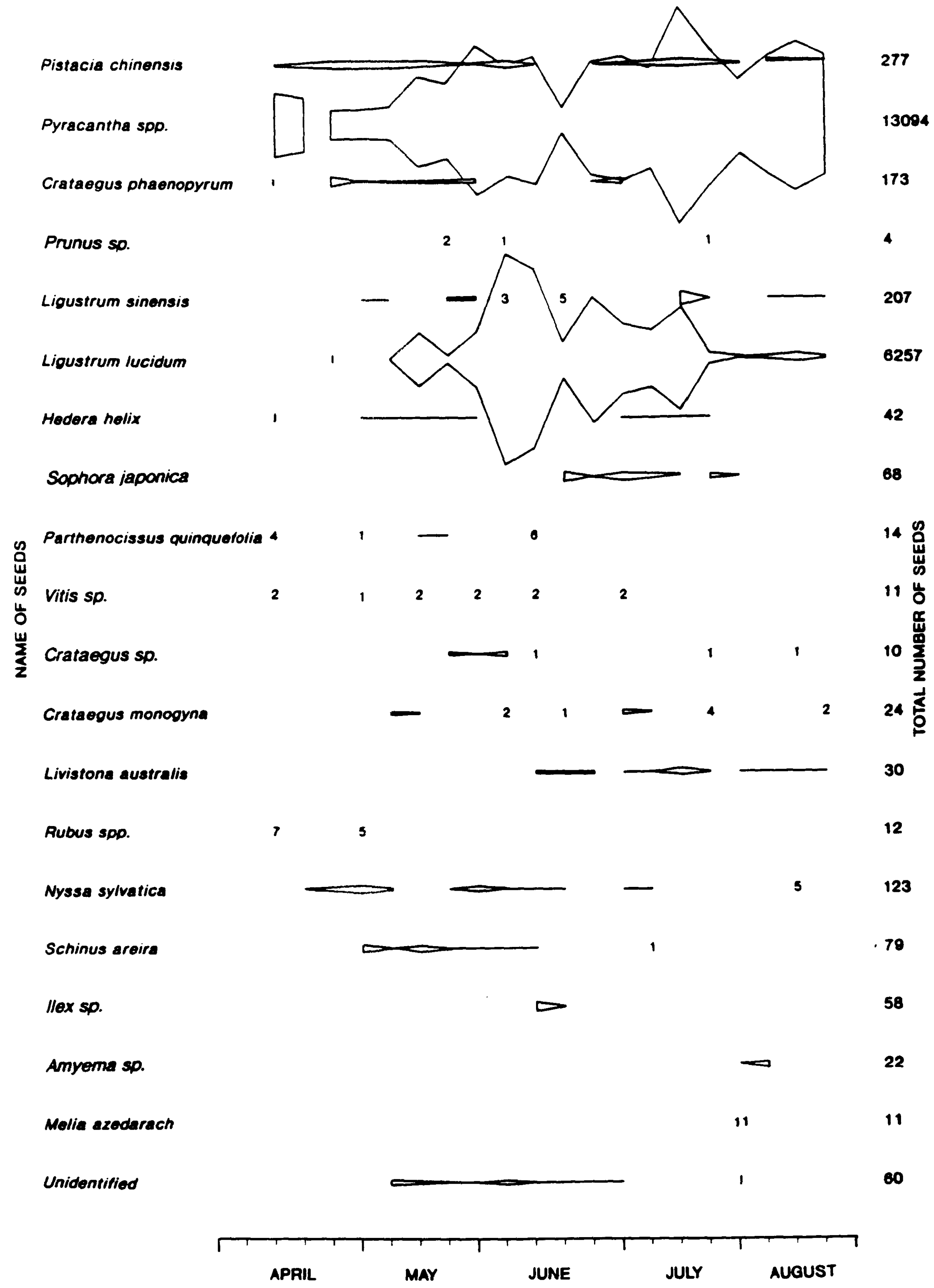

Figure 5.4 Seeds contained in Pied Currawong ejecta collected from a water tower located in the northern part of Armidale in 1989.

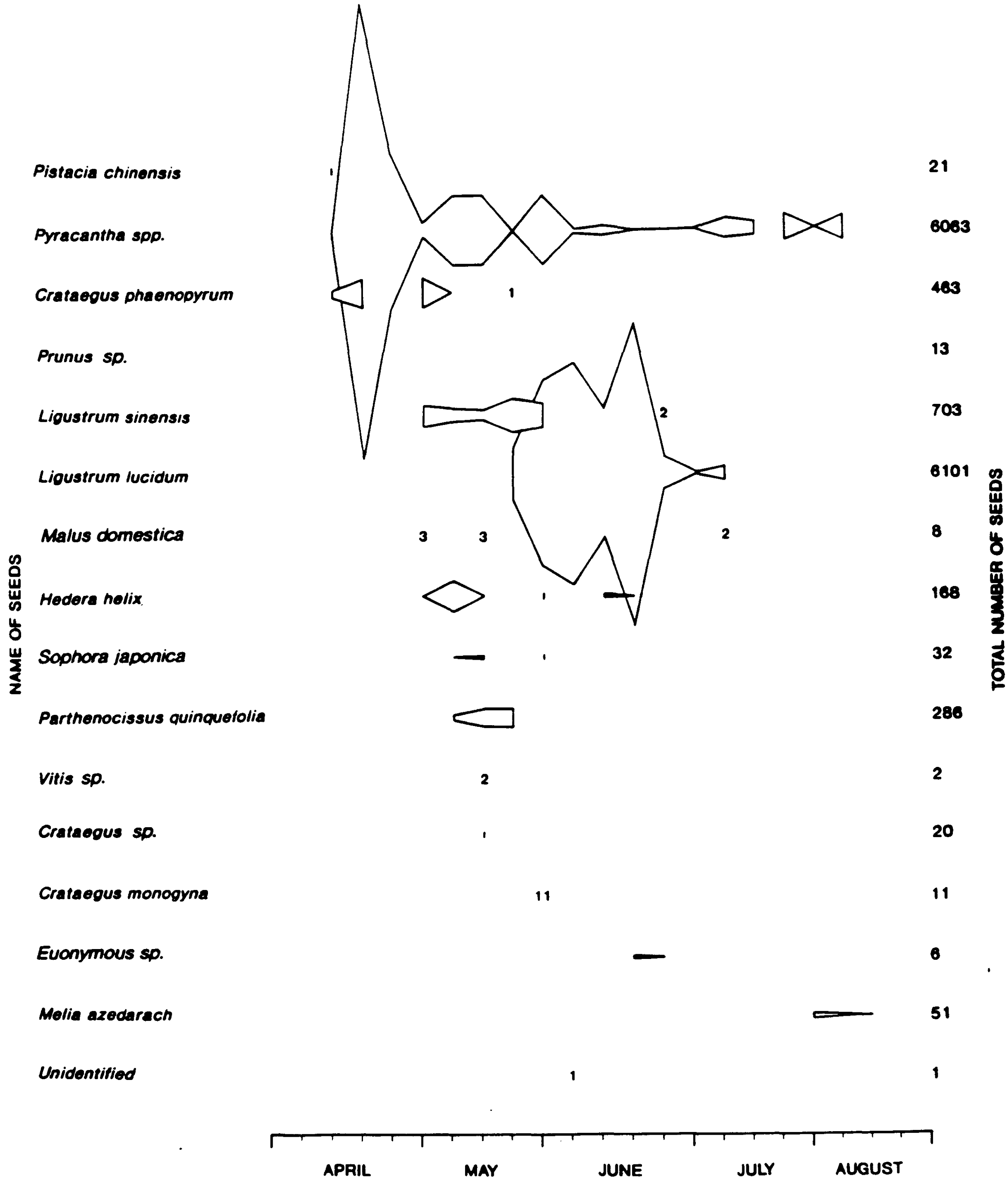

Figure 5.5 Seeds contained in Pied Currawong ejecta collected from a bird bath located under a *E.viminalis* tree near the Rockvale Road, Armidale in 1989.

closely reflects the ripening of fruit in Armidale (personal observations). However the pattern may also reflect non-random fruit selection by birds, based possibly on the nutritional status of fruit (Nakanishi 1991). Of note is the relatively small representation of *C.monogyna* in Pied Currawong diets. This will be discussed further in the light of further data.

5.4.4 Autumn-winter fruiting ornamental plants in Armidale

An assessment of the relative proportion of the major species planted in Armidale was obtained by the estimation of canopy volumes along either side of Markham Street, a major road running approximately north-south through the centre of Armidale. The transect was approximately 6 km long; the combined survey distance was *c.* 12 km. Ten metres in from the road side gutter all fruiting trees of the major species identified by the collection of Pied Currawong ejecta were recorded and the volume of their canopy estimated using width, breadth and depth of canopy. For plants forming hedges the length of hedge was also estimated. The canopy volumes were summed for each species and expressed as a percentage of the of the total canopy volume. This method did not distinguish between fruiting and non-fruiting canopies (e.g. between female and male plants, prereproductive and reproductive individuals). Where species were difficult to identify in the field, data was recorded at generic level. Canopy volumes were calculated for *C.monogyna*, *Pistacia chinensis*, *Pyracantha* spp., *Ligustrum* spp., *Cotoneaster* spp. and a category of 'others' which contained *Hedera helix*, *Rubus* (probably

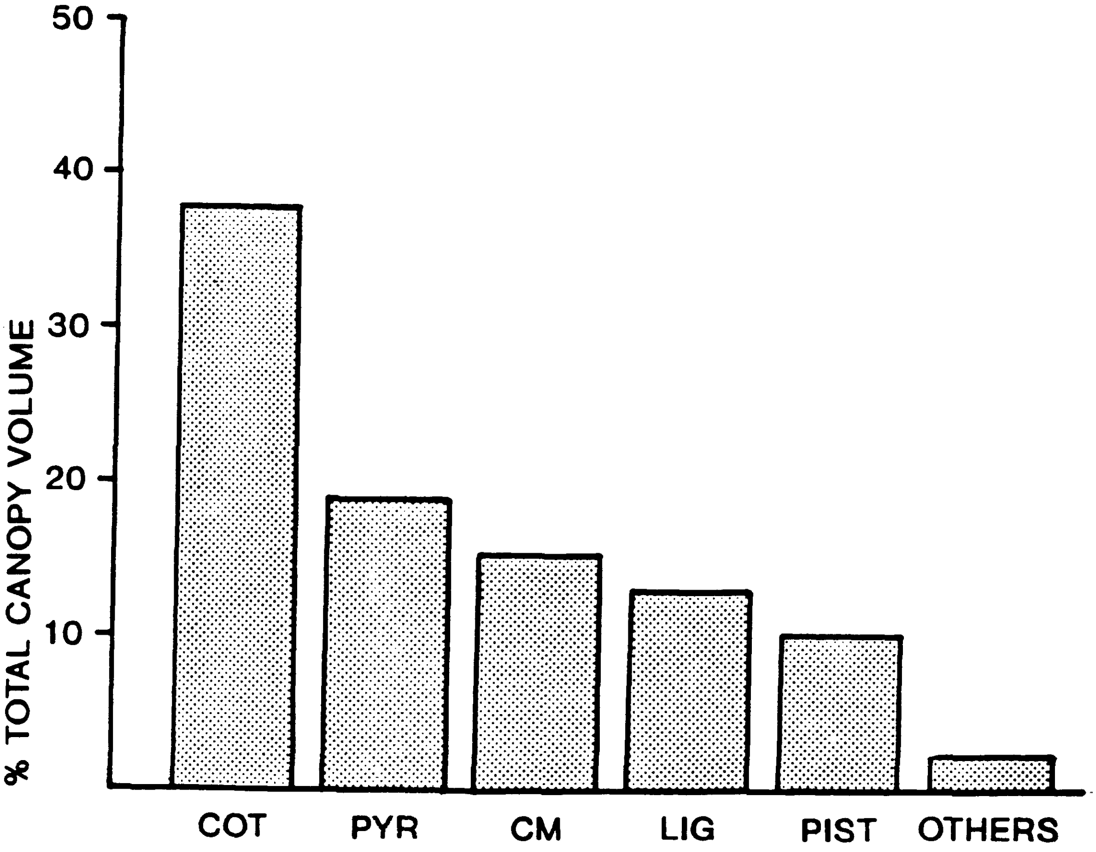

Figure 5.6 Proportion by volume of canopies of fruiting species of *Cotoneaster* (COT), *Pyracantha* (PYR), *C.monogyna* (CM), *Ligustrum* (LIG) *Pistacia* (PIST), and others from two parallel 6 km transects in the Armidale area in 1989.

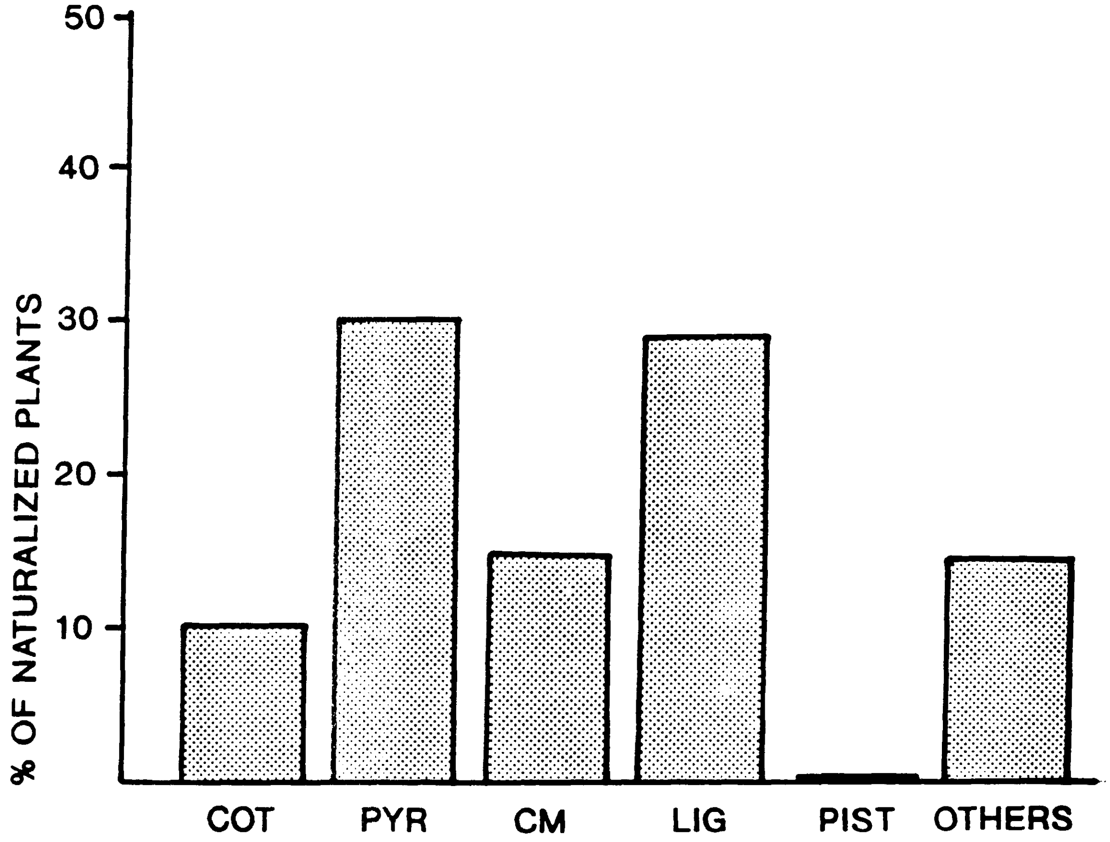

Figure 5.7 Proportion of fleshy fruiting taxa naturalised (or in the process of naturalization) in five sites around Armidale (from Smith unpublished data). The genera and species are the same as shown in Fig. 5.6. *Cotoneaster* (COT), *Pyracantha* (PYR), *C.monogyna* (CM), *Ligustrum* (LIG) *Pistacia* (PIST), and others

R.fruticosus), *Rosa* (mostly *R.rubiginosa*), *Malus, Prunus* (mostly *P.cerasifera 'nigra'*), and *Lonicera*.

Figure 5.6 shows the relative proportion that each species/genus contributes to the total canopy volume of fruiting ornamental species in Armidale. *Cotoneaster* contributes nearly 38%, followed by *Pyracantha, C.monogyna, Ligustrum, Pistacia* and 'others'.

Smith (unpublished data collected in October 1986, J.M.B. Smith *pers comm.* 1994. See Appendix 2) surveyed introduced fleshy and non fleshy fruiting woody plants >1 m tall, growing wild at six sites around Armidale. Two sites were located in the grounds of the University of New England where 219 and 345 plants were recorded; one site was located on the eastern outskirts of Armidale where 265 plants were recorded; one site in ASF with 228 plants; and two sites near the water tower on North Hill with 214 and 294 plants. I extracted from that data information specific to the same range of species in Figs. 5.4, 5.5 and 5.6.

Of the fleshy fruiting ornamental plants growing wild *Pyracantha* and *Ligustrum* were the most common, 30.4% and 29.4% respectively. *C.monogyna* is well represented, while *Cotoneaster* is relatively less common (see Fig. 5.7). So, despite widespread and intensive planting of *Cotoneaster* in Armidale compared to *Pyracantha* and *Ligustrum, Cotoneaster* does not appear to be a common component of Pied Currawong diets in Armidale, nor is it likely to become established in wild populations as much as *Ligustrum* and *Pyracantha*. This suggests the importance of effective seed dispersal for invasion by fleshy fruiting woody plants in Armidale.

The difference between high abundance of fruiting ornamental species and lower than expected appearance of their seeds in Pied Currawong diets, especially *C.monogyna* and *Cotoneaster*, may be due to intense interspecific competition between plants for attention of dispersers. It is possible that *Cotoneaster* has biochemical characteristics that make it relatively unattractive to Pied Currawongs, or perhaps that *Pyracantha* and *Ligustrum* have characteristics which make them more attractive. The fruits of *Pyracantha* and *Ligustrum* are smaller than those of *C.monogyna* which may make picking and ingesting them easier. *Pyracantha* and *Ligustrum* also have smaller seeds. Classic dispersal coevolution theory suggests that dispersers will select for smaller seed size to minimize the waste or 'ballast' costs of ingesting fruit (Howe and Smallwood 1982). Therefore the large fruit and seed of *C.monogyna* would be less attractive to birds. *Pyracantha* have very intense fruit displays and the small seeds are very easily separated from the fruit pulp by manipulation with fingers and therefore easier to process in bird guts. This is in contrast to *C.monogyna* fruit which are larger and the large seed they contain is more difficult to separate from the pulp. However the importance of these physical differences may not be critical given the relatively large body size (300 g) and gape width (1.85-1.95 cm) of Pied Currawongs.

Importantly with respect to *C.monogyna* is the historical context. Several decades ago *C.monogyna* may have been the most common part of Pied Currawong winter diets. In the early part of the century *C.monogyna* was one of only a few widely planted species of berry-bearing shrubs in Armidale and across the Northern Tablelands (see Chapter 3). During the mid and later parts of the twentieth century an influx of different ornamental species particularly of Asian origin such as *Pyracantha* offered a greater diversity of choice of potential food for birds. Interspecific competition between plants for dispersers may be a very important process in determining frugivorous patterns especially in respect to invasions by introduced floras (Knight 1986b, Debussche and Isenmann 1990).

Most of the plantings of *Cotoneaster*, *C.monogyna*, *Pyracantha*, and *Ligustrum* occur on private residential blocks. *P.chinensis* on the other hand is planted widely as a colourful and hardy street tree by the local council. The role of local government in the introduction of new species is not to be underestimated. Many small *P.chinensis* seedlings have appeared in surrounding bush and at ASF (D.Bass personal observations, Borgis 1993) and the species is therefore likely to increase in abundance. There are not represented in Fig 5.7 probably because most of the seedlings are still less than 1 m tall and were therefore not surveyed. *P.chinensis* fruits early in the year (March-April) and encounters little competition from other plant species for fruit ingestion by Pied Currawongs. A Pied Currawong killed by a car in early April 1989, and later dissected, had 49 whole and undamaged *P.chinensis* seeds in its crop. *P.chinensis* is likely to become more common in the Armidale region and may be a concern for environmental managers in the future.

5.4.5 Mammals

The role of mammals in the dispersal of fleshy-fruited plants in temperate regions is at best unclear. Studies in Europe and the Mediterranean document a role for mammals in the dispersal of a range of fleshy fruiting species (Herrera 1989, Debussche and Isenmann 1989) but relevant studies are few. Investigation of dispersal of *C.monogyna* seeds by mammals was undertaken by opportunistic collection of faeces in predominantly rural localities in the Armidale region. The range of species investigated included cattle (*Bos taurus*), sheep (*Ovis aries*), rabbits (*Oryctolagus cunniculus*), foxes (*Vulpes vulpes*), kangaroos and/or wallaroos (*Macropus* spp.) and Brush-tailed possums (*Trichosurus vulpecula*). Table 5.3 shows the number of *C.monogyna* seeds recovered from mammal faeces.

The collection of faeces was at best haphazard. As no sheep and cattle faeces collected during 1988 and 1989 contained *C.monogyna* seeds, little effort was directed at further work on these species. From time to time further faeces of these species were inspected for seeds during the *C.monogyna* fruiting season and no seeds were ever found. Rabbits and macropods were found to only occasionally disperse *C.monogyna* seeds. Brush-tailed possums on the other hand had a relatively high incidence of *C.monogyna* fruit ingestion and seed dispersal. Bass (1990) detailed the collection of faecal pellets of Brush-tailed possums from under the canopies of *Eucalyptus* and *Pinus radiata* trees and from ASF, the Saleyards and from the grounds of the University of New England (UNE). The mean number of fruit stones per faecal pellet calculated from pellets containing *C.monogyna* seeds ranged from 1.73 ± 0.91 (N = 64 pellets) at the UNE to 3.96 ± 2.26 at ASF (N = 57 pellets).

Table 5.3 Analysis of mammal faeces collected in the Armidale region from 1988 to 1991.

Mammal species	Number of faeces collected	Number of *C.monogyna* seeds	Distance to nearest fruiting *C.monogyna* (m)
Cattle	21	0	-
Sheep	153	0	-
Rabbit	97	5	20
Fox	32	23	5-35
Macropod	58	19	10-45
Possum	290	484	0-50

The overall role of dispersal by mammals, and the individual importance of each mammal species, are difficult to assess. No actual observation of feeding on *C.monogyna* fruit was documented. As the collection of faeces was opportunistic only inferences on the type of seed dispersal shadow resulting from mammal dispersal can be made. In the case of sheep and cattle the fact that no seeds were found in their faeces does not mean that they never disperse seeds. Hatton (1989) found that sheep occasionally dispersed seeds of *Rosa rubiginosa*. Rabbits and macropods were shown to occasionally disperse intact seeds of *C.monogyna*, but this was apparently not common. Foxes, reported to ingest *C.monogyna* elsewhere (Lloyd 1980) also occasionally do so in Australia. Brush-tailed Possums were relatively important dispersers.

Differences between the mammals and how they interact with *C.monogyna* can explain the differences in the occurrence of *C.monogyna* seeds in their faeces. *C.monogyna* has persistent fruit; the fruits remain attached to the peduncle and remain in the canopy for long periods. Consequently there is little fruit dropped under the parent tree until it is substantially desiccated. Save for the possums, all the mammals studied are predominantly ground foragers. Therefore *C.monogyna* fruit is unlikely to be in a position to become incorporated in their diet on a large scale, and when it does it is possible that it is ingested more by accident that intentionally. As *C.monogyna* is deciduous and no leaves are present on plants for most of the period when ripe fruit is available, the ingestion of fruit by arboreal possums is not likely to be accidental.

The distance of seed-containing faecal pellets from the nearest fruiting *C.monogyna* tree was the only measure available for estimation of dispersal distance. For rabbits this was < 20 m; foxes < 35 m; macropods < 45 m; and possums < 50 m. These can only provide conservative dispersal distance estimates. Home ranges and the distances travelled by the various species vary considerably. Possums have been documented travelling up to 1600 m on feeding forays (Jolly 1976), however Crawley (1968) suggested that most movements within home ranges by possums are < 100 m. Movements by rabbits within their home ranges vary from *c.* 50 m up to several hundred metres (Myers and Poole 1959). Macropods and foxes on the other hand may move many kilometres (Strahan 1983).

The general scenario of seed dispersal of *C.monogyna* and the process of range expansion can be visualized as a series of stages beginning with planted hedges or individual plants in gardens. These act as multiple foci (see discussion in Chapter 3, Mack (1985), Moody and Mack (1988)). Pied Currawongs attracted to this food source would ingest seeds and disperse seeds over many kilometres. Dispersal by Pied Currawongs is commonly to places beneath tall trees used as perching sites, as indicated by the occurrence of hawthorn and other bird-dispersed introduced shrubs particularly beneath rather than between trees in the Armidale area (Smith 1982). Fence lines and telegraph poles offer perch sites in the same way. The seeds germinate and grow into mature fruiting individuals, and may thereby produce satellite foci on which both Pied Currawongs and possums feed. The main effect of the possums would be to fill in the gaps between these scattered first generation wild plants resulting from dispersal by birds.

5.5 *Prunus mahaleb*

5.5.1 Bird facilitated seed dispersal

Observations of seed dispersal of *P.mahaleb* were mainly carried out between 5 and 18 January 1990. Supplementary information was collected during the corresponding fruiting periods of 1988 and 1989. During the summers of 1989 and 1990 the researcher was on crutches and his mobility severely impeded. As a result, detailed observations of bird feeding behaviour during these periods were made only at a single *P.mahaleb* tree. The tree was selected on the basis of access for the researcher as well as its apparent representativeness of other *P.mahaleb* in the area.

Casual observations in 1988, 1989, 1990 and 1991 were used to establish the range of avifauna in the study area during the *P.mahaleb* fruiting period, and which birds consumed *P.mahaleb* fruit (Table 5.4).

Three types of observation were used to monitor visitation, feeding behaviour and post-feeding flight distances. First, consecutive one minute observations were made. For the first 30 s of each minute all birds in the tree were located and identified. In the following 30 s a count of all birds present, including new arrivals was made. For each species the total number of birds recorded for each observation was summed and then divided by the total number of observations to derive a visitation index (VI) for each species.

Table 5.4 List of all birds seen in the ASF study area both in and out of the formal observation period. Birds seen feeding on *P.mahaleb* are indicated by SP for seed predator, PP for pulp predator and D for disperser based on field observations. Names follow the nomenclature of Blakers *et al.* (1984).

Family Species	Feeding behaviour
Falconidae	
Australian Hobby *Falco longipennis*	-
Platycercidae	
Crimson Rosella *Platycercus elegans*	SP
Eastern Rosella *Platycercus eximius*	SP
Culculidae	
Horsefield's Bronze Cuckoo *Chrysococcyx basalis*	-
Alcedinidae	
Laughing Kookaburra *Dacelo novaeguineae*	-
Coraciidae	
Dollarbird *Eurystomus orientalis*	-
Muscicapidae	
Eastern Yellow Robin *Eopsaltria australis*	-
Crested Shrike-tit *Falcunculus frontatus*	-
Golden Whistler *Pachycephala pectoralis*	D
Rufous Whistler *Pachycephala rufiventris*	D
Grey Shrike-thrush *Colluricincla harmonica*	-
Grey fantail *Rhipidura fulignosa*	-
Maluridae	
Superb Fairywren *Malurus cyaneus*	-
Acanthizidae	
Yellow-rumped Thornbill *Acanthiza chrysorrhoa*	-
Meliphagidae	
Red Wattlebird *Anthochaera carunculata*	D
Noisy Friarbird *Philemon corniculatus*	D
Yellow-faced Honeyeater *Lichenostomus chrysops*	PP
Eastern Spinebill *Acanthorhynchus tenuirostris*	PP
Dicaeidae	
Mistletoebird *Dicaeum hirundinaceum*	D
Zosteropidae	
Silvereye *Zosterops lateralis*	D
Ploceidae	
Red-browed Firetail *Emblema temporalis*	-
Double barred Finch *Poephila bichenovii*	-
Oriolidae	
Olive-backed Oriole *Oriolus sagittatus*	D
Corcoracidae	
White-winged Chough *Corcorax melanorhamphos*	-
Cracticidae	
Grey Butcherbird *Cracticus torquatus*	-
Australian Magpie *Gymnorhina tibicen*	-
Pied Currawong *Strepera graculina*	D
Corvidae	
Australian Raven *Corvus coronoides*	D

The second set of observations followed in part the methodology of Herrera and Jordano (1981). The length of stay in the tree and the number of fruits ingested for each bird species was recorded. A full observation was achieved when a bird was observed uninterrupted from the moment it entered the tree to when it left. If a continuous view of a bird was not possible (e.g. the view was obscured by foliage) then that observation was recorded as a partial observation. Only full observations were used to calculate the average duration of visits and fruit ingestion rate for each species.

The third set of observations recorded post-feeding flight distances for each species. The distance a bird flew from the feeding tree to the point where it first landed was taken as the post-feeding flight distance and was estimated to the nearest 5 m. A small set of observations in 1988 recorded post-feeding flights which also included a directional component for Noisy Friarbirds at a different *P.mahaleb* tree.

The methods used by birds to void seeds (regurgitation or defecation) was also recorded. When located, voided seeds were examined for damage which would indicate seed predation. Birds of twelve species were observed consuming *P.mahaleb* fruit. Of these Crimson Rosellas *Platycercus elegans* and Eastern Rosellas *P.eximius* killed seeds by cracking open the fruit stones and crushing and eating the seeds. These birds represent seed predators. Two species (Yellow-faced Honeyeaters *Lichenostomus chrysops* and Eastern Spinebills *Acanthorhynchus tenuirostris*) ate the fruit pulp without ingesting any seeds. Seeds were left attached to the peduncle or were knocked to the ground beneath the fruit canopy. These birds represent pulp predators. Two birds, Rufous Whistlers *Pachycephala rufiventris* and the Australian Raven *Corvus coronoides* were seen eating *P.mahaleb* fruit on a few occasions but never during the main observation period. Birds of six species were observed ingesting whole *P.mahaleb* fruit at the study tree during the observation period (Table 5.5).

On average 2.24 birds were recorded per observation. By far the most frequent visitors were Noisy Friarbirds (visitation index VI 1.24) which accounted for 55.3% (N = 693) of all records. Red Wattlebirds and Silvereyes were the next most frequent visitors (VI 0.38 and 0.33 respectively).

Table 5.5 Visitation index for birds visiting a single *Prunus mahaleb* tree, Armidale State Forest, January 1990. (Birds listed in order of body size, see Table 5.6).

	number of birds	% total all species	visitation index
Pied Currawong *Strepera graculina*	25	1.9	0.05
Red Wattlebird *Anthochaera carunculata*	214	17.1	0.38
Noisy Friarbird *Philemon corniculatus*	693	55.3	1.24
Olive-backed Oriole *Oriolus sagittatus*	65	5.2	0.12
Silvereye *Zosterops lateralis*	184	14.7	0.33
Mistletoebird *Dicaeum hirundinaceum*	73	5.8	0.13
Total	1254	100.0	2.24

Table 5.6 shows the average duration of visit, the number of full observations, the fruit ingestion rate and the average number of whole fruit ingested per feeding event calculated by multiplying the ingestion rate by the average duration of visit for each species.

Table 5.6. Body mass and foraging statistics of the avian fruit eaters of *P.mahaleb* at ASF. Sample sizes are shown in parentheses.

	Mean body mass (g)*	Length of visit (s)$^{+}$	Fruits ingested per minute^{++}	Fruits ingested per visit^{+} [maximum]
Pied Currawong *S.graculina*	300.0	140.0 (1)	10.3 ± 3.0(5)	23.0 (1) [23]
Red Wattlebird *A.carunculata*	125.0	121.6 ± 38.7 (8)	4.2 ± 2.0(17)	10.0 ± 5.3 (8) [16]
Noisy Friarbird *P.corniculatus*	107.0	109.8 ± 80.1(19)	4.4 ± 3.4(54)	7.0 ± 4.8 (19) [17]
Olive-backed Oriole *O.sagittatus*	96.0	64.7 ± 8.3 (3)	6.2 ± 3.2 (9)	8.0 ± 2.2 (3) [10]
Silvereye *Z.lateralis*	10.3	24.2 ± 7.6 (6)	2.0 ± 2.8(22)	0.8 ± 0.4 (6) [1]
Mistletoebird *D.hirundinaceum*	8.0	17.8 ± 42.2 (5)	1.5 ± 2.5(10)	0.6 ± 0.5 (5) [1]

* From Ford and Bell (1981)

\+ Calculated from full observations

++ Calculated from full and partial observations

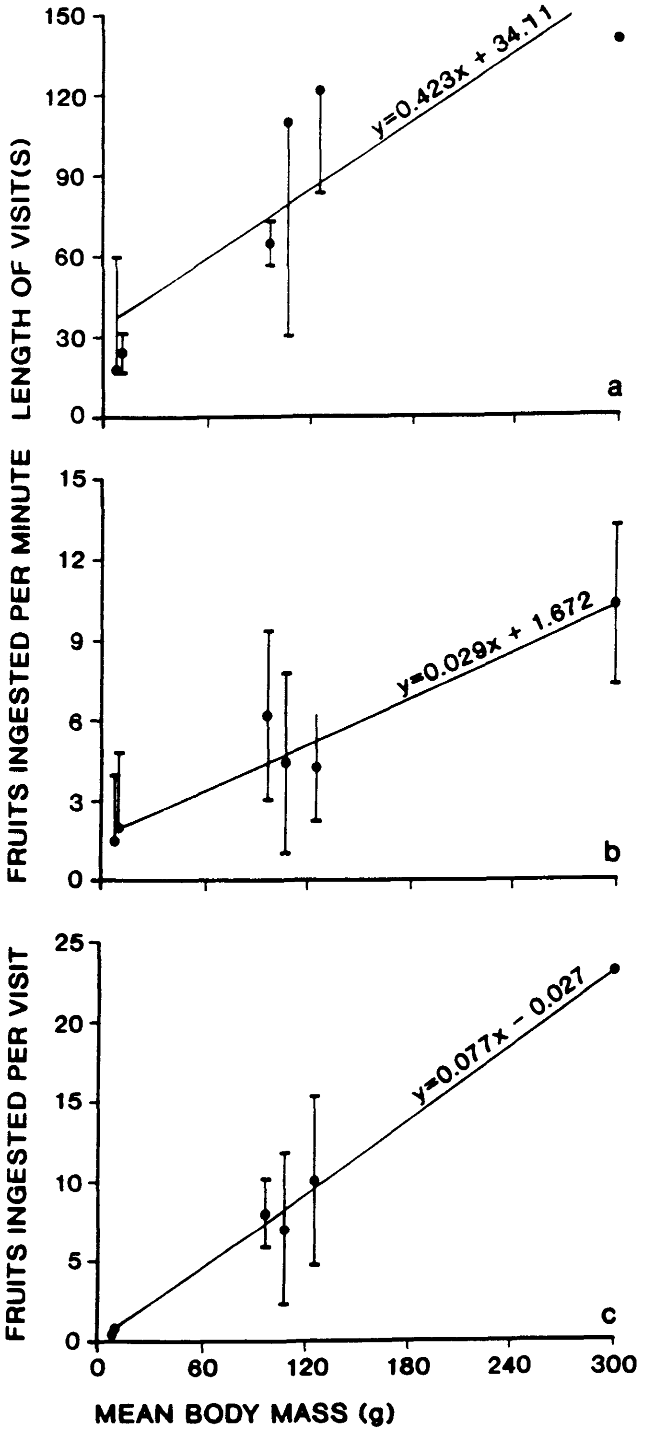

Figure 5.8 Relationships of mean body mass in grams to (a) length of visit of birds in seconds, (b) the number of fruits ingested per minute, and (c) average number of fruit ingested per visit. Data from a single *P.mahaleb* shrub during 5-18 January, 1990, Armidale State Forest. Vertical bars are standard deviations. Where there are no bars the same size or deviations are too small to represent on the scale. Half bars are used where deviations extend beyond the scale of graphs.

For all species, body weight was positively correlated with length of visit (Fig. 5.8(a): $r^2 = 0.758$), fruits ingested per minute (Fig. 5.8(b): $r^2 = 0.912$), and fruits ingested per visit (Fig. 5.8 (c) :$r^2 = 0.994$). The Pied Currawong at 300.0 g was the largest bird, which stayed the longest in the tree (140.0 s), ingested fruit the fastest (10.3 fruit per minute) and ingested the most fruit per visit (23.0 fruit).

The small number of observations for Pied Currawongs in Table 5.6 was supplemented by analysis of regurgitated pellets found in the study area during the period of observations. Of 17 part or whole pellets 333 whole *P.mahaleb* seeds were recovered at an average of 19.6 ± 9.2 seeds per pellet (range 4-40 seeds). Pied Currawongs at this summer season do not fly long distances during their diurnal feeding activities, nor return at night to a communal roost, as they do in winter (see section 5.3.2). Instead, they appear to restrict their movements to within local breeding territories. They are therefore unlikely to transport *P.mahaleb* seeds over such long distances as they do other species including *C.monogyna* which fruit in winter.

Of the birds recorded ingesting *P.mahaleb* fruit their feeding behaviour included two techniques. First, some birds detached fruit from the peduncle and swallowed the fruit whole. In the second technique, fruit were detached from the peduncle and thrashed against a branch. The pulp was eaten and the seed allowed fall to the ground beneath the shrub canopy. Larger birds, such as Pied Currawongs, Red Wattlebirds, Olive-backed

Orioles and Noisy Friarbirds, ingested most of the fruit with which they came into contact, while smaller birds like Silvereyes and Mistletoebirds utilized both feeding techniques, generally dropping more fruit than they ingested (Tables 5.7, 5.8).

Table 5.7. Successful feeding attempts of the birds at ASF. N = number of observations.

	N	Percentage of fruit	
		Ingested	Dropped
Pied Currawong *S.graculina*	5	100.0	0.0
Red Wattlebird *A.carunculata*	17	94.8	5.2
Noisy Friarbird *P.corniculatus*	54	87.8	12.2
Olive-backed Oriole *O.sagittatus*	9	100.0	0.0
Silvereye *Z.lateralis*	22	35.5	64.5
Mistletoebird *D.hirundinaceum*	10	27.8	72.2

Noisy Friarbirds and Red Wattlebirds were often observed flicking their tongue against *P.mahaleb* fruit, apparently tasting the juice. Some fruits were rejected and the process continued until a fruit was swallowed.

Table 5.8. The number of fruit ingested and dropped while feeding by each species calculated by multiplying the number of birds seen in the 560 observations by the average number of fruits ingested per visit and the feeding success rate form table 5.7.

	Number of fruit ingested	Number of fruit Dropped
Pied Currawong *S.graculina*	575.0	0
Red Wattlebird *A.carunculata*	2140.0	117.4
Noisy Friarbird *P.corniculatus*	4851.0	674.1
Olive-backed Oriole *O.sagittatus*	520.0	0
Silvereye *Z.lateralis*	147.2	267.4
Mistletoebird *D.hirundinaceum*	43.8	113.7

Noisy Friarbirds began to defend the *P.mahaleb* tree toward the end of the observation period when fruit became more scarce. Nineteen separate episodes involved Noisy Friarbirds driving off other birds including Red Wattlebirds (N = 8), Yellow-faced Honeyeaters (N = 5), Olive-backed Orioles (N = 3), Silvereyes (N = 2) and a Mistletoebird.

In total 219 post-feeding flight observations were made. The proportional representation of each species was not significantly different to that recorded in Table 5.2 (X^2 = 6.73, d.f. = 5, $P < 0.01$). Figure 5.7 shows post-feeding flight distances for each species. No bird was observed flying more than 70 m. However, it should be emphasized that these observations were only of initial post-feeding flights: any subsequent flights are likely to result in more distant seed dispersal in many cases. In general though once a bird had settled on a perch and began to process its meal of fruit and seeds, it usually remained there until it voided its load of seed. The time spent perching between feeding events was commonly between 15 and 30 minutes.

As the number of post-feeding flights recorded for each species is roughly proportional to the visitation rates, it is feasible to construct a conservatively estimated seed shadow of avian dispersed seeds. By multiplying average fruit ingested per visit (Table 5.6) and frequency of post-feeding flight distances for each species (Fig. 5.9) and summing for all species a picture of a seed dispersal shadow based on distance from the fruiting tree evolves. Figure 5.10 shows the resultant seed shadow. The log of seed number was highly negatively correlated with distance from the *P.mahaleb* tree ($r = -0.938$, d.f. = 10, $P < 0.01$).

The Noisy Friarbird was the species of bird most frequently observed feeding on *P.mahaleb* fruits. They accounted for nearly 60 % of all fruit ingested (calculated from Table 5.8). Noisy Friarbirds only flew to tall eucalypts and pines, avoiding the very common, smaller wattle (*Acacia*) shrubs. This indicates that post-feeding flights are affected by the surrounding vegetation structure. Noisy Friarbirds will fly to large trees where they can remain inconspicuous while

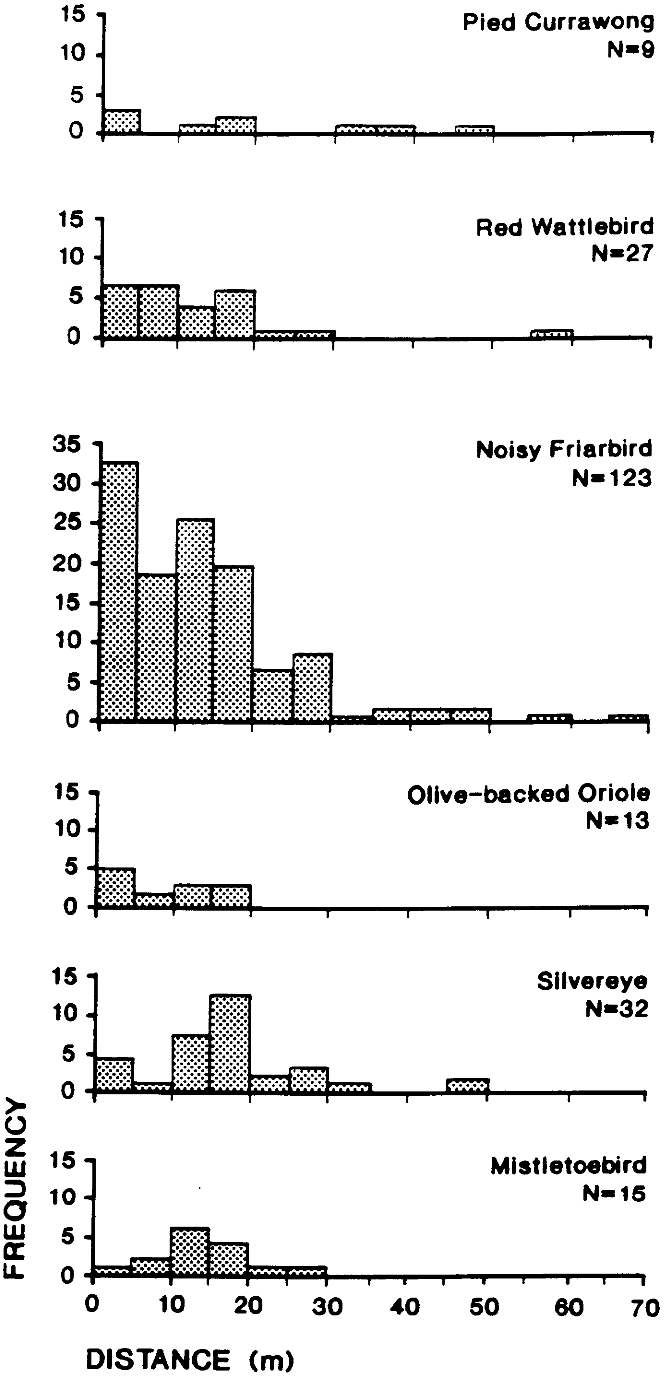

Figure 5.9 Frequency of post-feeding flight distances of birds ingesting *P.mahaleb* fruit 5-18 January, 1990. N is the number of observations.

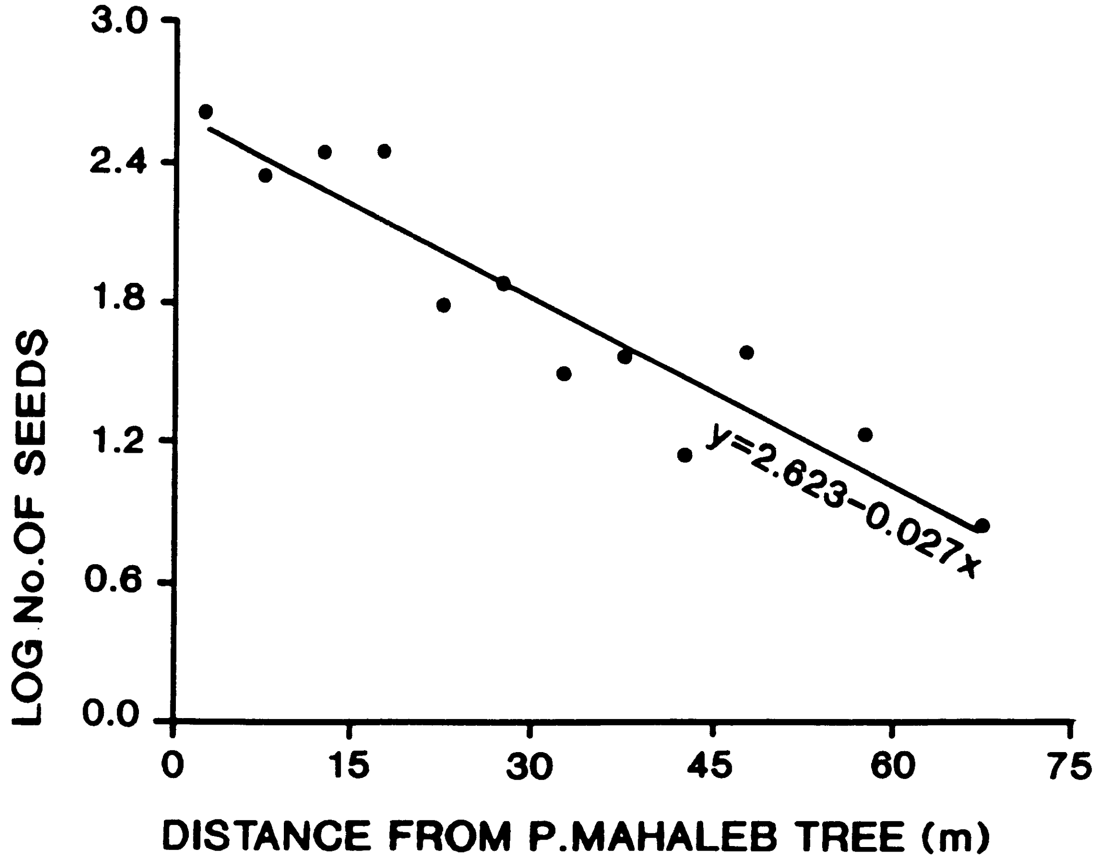

Figure 5.10 Seed dispersal shadow for *P.mahaleb* in ASF, derived from Table 5.6, Fig. 5.9. See explanation in text.

processing their meal, void seeds and then return to feed. Very few *P.mahaleb* trees at the site occur in open paddocks, most being located in woodlands and amongst *P.radiata* trees. Therefore Noisy Friarbirds after feeding on *P.mahaleb* fruit do not have to fly long distances in order to arrive at adequate safe perches. A consequence of this pattern of behaviour of the most important disperser in terms of quantities of seeds dispersed is that *P.mahaleb* seeds are not likely to be dispersed over large distances.

5.5.2 Mammal facilitated seed dispersal

Opportunistic observations and collection of mammal faeces was conducted each day during, and during the week after, the 1990 fruiting season. For each sample of faeces the species responsible, site of deposition and condition of seeds were recorded. These collections were supplemented with data from 1989. For the purposes of this study whole undamaged seeds were regarded as viable.

Faeces from rabbits *O.cuniculus*, Brush-tailed possums *T.vulpecula* and foxes *V.vulpes* were collected and examined for *P.mahaleb* seeds. Table 5.9 lists the number of seeds found in faeces and the distance to the nearest fruiting *P.mahaleb* tree.

Table 5.9 The number of *P.mahaleb* seeds collected from rabbit, fox and possum faeces at ASF.

Mammal species	Number of faeces collected	Number of *P.mahaleb* seeds	Distance to nearest fruiting *P.mahaleb* (m)
Rabbit	761	617	0-35
Possum	54	205	0-30
Fox	6	26	0-250

Of 761 rabbit faecal pellets collected, 323 contained 617 *P.mahaleb* seeds at an average of 1.9 0.9 seeds per pellet (range 1 - 5). Seed-containing pellets were found 0 - 35 m from the nearest fruiting *P.mahaleb* tree. Faeces were generally deposited on dung hills but occasionally faeces were found on bare ground and lodged in rock crevices away from dung hills. Fragments of fruit stones estimated to be equivalent to 29.5 stones were found in 50 faecal pellets, indicating a predation rate of 8.4% of all fruit stones found.

Of 54 possum faecal pellets collected, 49 contained 205 whole *P.mahaleb* seeds at an average of 4.2 ± 2.0 seeds per pellet (range 1 - 9). Possum faeces were only found under the canopies of *P.radiata* trees. Seed-containing pellets were found 0 - 30 m from the nearest fruiting *P.mahaleb* trees. No damaged seeds were found.

On three evenings a spot light was used to locate possums in the study area. Two Brush-tailed possums were seen, both in *P.radiata* trees close to fruiting *P.mahaleb* trees.

Six fox faeces containing 26 *P.mahaleb* seeds were found. Three were found on gravel roads, two under pine trees and one on open rocky ground at distances ranging from 0 - 250 m from the nearest fruiting *P.mahaleb* tree. Faeces also contained insect exoskeletons and 52 seeds of *Prunus cerasifera* at distances ranging from 10 - 150 m from the nearest fruiting *P.cerasifera* tree. No damaged seeds were found.

Foxes were regularly seen in the study area. On one afternoon a fox was observed with 10x binoculars moving between clumps of *P.mahaleb*, feeding on fallen fruit. One morning a fox was observed leaving the study area carrying part of a dead rabbit in its jaws. It is possible in the light of the previous section that secondary dispersal of seeds may be facilitated by ingestion of rabbits which may in turn have a seed load in their intestinal tract. A similar instance was reported by Somerset (1975) in relation to weed flora established under a Wedge-tailed Eagles' nest. Rabbits feeding on pasture weeds were killed by wedge-tailed Eagles, their carcasses carried to the nest, and seeds contained in the rabbits' digestive tract were deposited below the nest.

5.6 Comparison of *Crataegus monogyna* and *Prunus mahaleb* dispersal ecologies.

A direct quantitative comparison between *P.mahaleb* and *C.monogyna* is difficult based on the differing methodologies that needed to be used. In particular there is a problem quantifying the dispersal of *C.monogyna* seeds. However, despite this short-coming important differences are apparent.

Crataegus monogyna has a long fruiting season. Therefore it has a diffuse pattern of fruit availability. During autumn and winter a number of other exotic plant species also produce fleshy fruit. The competition for a dispersal agent is consequently more intense (Sorenson 1981). The main seed disperser is the Pied Currawong. This gregarious bird is large, can ingest many fruit, is capable of flying long distances, and represents an effective dispersal agent for *C.monogyna*. Mammals such as macropods and foxes are also large, mobile animals. They move over large distances and represent potentially important secondary dispersers. However the pattern of vertebrate seed dispersal found in this study does not appear to adequately explain the very wide distribution of *C.monogyna* seen today, more particularly the amount of *C.monogyna* seed dispersed compared to other, currently less invasive species fruiting at the same time. There is today a distinct lack of distantly dispersed seedlings, which contrasts with the abundance of mature wild shrubs over large areas. The explanation may involve a change in dispersal activity for *C.monogyna*. During the late nineteenth and early twentieth centuries *C.monogyna* was a commonly planted ornamental and hedge plant. It was actively planted as a cheap means of fencing being a hardy plant admirably suited to the tablelands environment (see Chapter 3). As the plants matured they produced vast crops of fruit. This represented a new food resource for many birds and animals, available for several months each year, in an area which had suffered large scale clearance for agriculture and which in any case had a limited range of winter fruiting native plants.

Pied Currawongs would have benefitted greatly from this new source of food, in much the same way that cultivated and ornamental plants in the Montpellier region in France allow birds to winter in more northern and different areas than they formerly used (Debussche and Isenmann 1990). Pied Currawongs would have facilitated rapid and widespread range expansion of *C.monogyna*. This picture has changed with the introduction and spread of a much wider range of fleshy fruiting ornamental plants such as species of *Ligustrum*, *Pyracantha* and *Pistacia* (see Figs 5.4 and 5.5). These species appear to have traits which make them more attractive to Pied Currawongs and so the consumption of *C.monogyna* fruit has dropped. As seen in Figs 5.4 and 5.5 *C.monogyna* seeds are now represented quite poorly in Pied Currawong diets despite this being an abundant plant (Figs 5.6, 5.7).

Prunus mahaleb on the other hand displays a well developed dispersal system, comparable with its performance within its native range. The diversity of dispersers provide a variety of dispersal quality likely to facilitate local range expansion of *P.mahaleb* near Armidale. To examine how effective the dispersal of *P.mahaleb* in Australia is, it is useful to compare the Armidale data with that obtained for *P.mahaleb* in its native range in Europe. Herrera and Jordano (1981) provided detailed information on the avian dispersal system of *P.mahaleb* with some anecdotal information for mammals. Reference to dispersal of *P.mahaleb* seeds, particularly in relation to fruit traits, appears in Herrera (1987, 1989) and Debussche and Isenmann (1989). In these studies it was shown that a variety of birds and ground-dwelling mammals dispersed *P.mahaleb* seeds, though these agents differed in quality and quantity of dispersal.

Herrera and Jordano (1981) identified six avian seed dispersers, two of which were regarded as rare and thus relatively unimportant. The majority of seed dispersal occurred over distances < 50 m which is comparable to dispersal distances achieved in Australia. The Stone Marten *Martes foina* along with *Vulpes vulpes* were later identified as important carnivorous seed dispersers (Herrera 1989, Debussche and Isenmann 1989). Guitian *et al.* (1992) reported 16 species of birds perching in fruiting trees, swallowing whole fruits, carrying fruit away, dropping fruit and cracking seeds open in *P.mahaleb* trees. By comparison the present study revealed eight birds (two of which were recorded only outside the period of detailed observation) and two mammals (one being arboreal) were recorded dispersing *P.mahaleb* seeds in Australia.

Seed dispersal of *P.mahaleb* is over distances generally less than 100 m, with a significant proportion of fruit falling beneath parent plants due to natural fruit fall, and as a result of unsuccessful feeding attempts by birds. Long-distance seed dispersal is relatively rare. The seed dispersal system of *P.mahaleb* results in high seedling densities near and under parent plants thereby promoting a slower rate of spread compared to *C.monogyna*.