

## CHAPTER 1: INTRODUCTION

This thesis is divided into three main parts. The first (Chapters 1 and 2) address biological invasions in the global and Australian context. It outlines the nature and processes of biological invasions and presents aspects that characterize successful invasions. Within this context, the current project, study species and region are described. The second part documents the rate of spread (Chapter 3), demography (Chapter 4), and seed dispersal ecology (Chapter 5) of both species. The third section discusses the results of this thesis within the context of which factors determine the invasiveness of introduced fleshy fruiting woody plants in southeastern Australia.

### 1.1 Biological invasions: introduction and literature review.

A biological invasion occurs when an organism arrives naturally or is transported, usually accidentally or intentionally by humans, colonizes and spreads into new territories some distance from its home territory (di Castri 1990). Biological invasions are responsible for the development of regional biotas and, increasingly under the influence of humans have profound implications for: maintenance of global biodiversity; agriculture; and human health to name just a few (di Castri 1990).

To illustrate the importance of biological invasions it is useful to briefly recall some of the impacts of the invasion of Australian ecosystems by just one of the thousands of introduced species, the European Rabbit (*Oryctolagus cuniculus*). Originally native to the Mediterranean region, rabbits were introduced to Australia from Britain in 1858-1859 and then a number of times thereafter (Myers 1983, Rolls 1969). Rabbits were relatively well adapted to the Australian environment. They benefitted from forest and woodland clearance for agriculture, the establishment of pastures, and the earlier development of a low sward through grazing by sheep (Jarman 1986). There were relatively few predators, many of which were maladapted to the human modifications of the environment. Rabbits caused a great deal of disturbance through burrowing and grazing. This disturbance has led to accelerated soil erosion (McTainsh and Boughton 1993, Macdonald *et al.* 1989). Modification of the vegetation has also accompanied soil erosion. Predation on seedlings of various native shrubs, for example *Acacia burkittii* (Crisp and Lange 1976), has reduced the recruitment and sounded the death knell for some species. Rabbits have caused great ecological as well as considerable geomorphological change which have combined to represent a significant economic burden on Australia.

Rabbits spread rapidly, visibly and in an economically conspicuous way in Australia; thousands of other species are also invading (Groves and Burdon 1986), often less rapidly and

conspicuously, but in many cases just as significantly from an ecological viewpoint. The present study aims to advance understanding of the biological invasion process, with particular reference to two woody plant species.

Biological invasions have been the focus of a wealth of published works during the 1980s and early 1990s. Much of the interest arose out of the Scientific Committee on the Problems of the Environment (SCOPE) project "Ecology of Biological Invasions". The project was initiated in June 1982 and was set to address three main questions: (1) what are the factors that determine whether a species will be an invader or not? (2) what are the site properties that determine whether an ecological system will be relatively prone to, or resistant to, invasion? and (3) how should management systems be developed using the knowledge gained from answering these questions? (Drake *et al.* 1989).

Most notable of the biological invasion publications arising out of SCOPE are the series of books and special issues of works from South Africa (Macdonald *et al.* 1986), the United Kingdom (Kornberg and Williamson 1986), Australia (Groves and Burdon 1986), the United States of America (Mooney and Drake 1986) and Europe (di Castri *et al.* 1990). There are many more works that address biological invasions in an applied way and at a regional scale (for example Kitching 1986, Humphries *et al.* 1991 for Australia, and Groves and di Castri 1991 for Mediterranean ecosystems). However it is Drake *et al.* (1989) that brings together SCOPE's aim of a global perspective.

### 1.1.1 Terminology of biological invasions.

The broad term "biological" encompasses vertebrate and invertebrate animals, plants and micro-organisms. The terminology used to describe invasions has been largely subjective and as such inconsistently applied (Groves and Burdon 1986). This section seeks to clarify the terminology and review recent research overseas and in Australia.

A **biological invader** is an organism that has been brought intentionally or unintentionally by humans to areas outside of its natural range (di Castri 1990). This is synonymous with **introduced species, alien, exotic** and in some instances **translocated species** (see Shafland and Lewis 1984). This approach implicitly recognizes the important role of humans as agents of introduction. However it ignores causes of 'natural' invasion which form the basis of biotic exchange between biogeographic regions prior to the appearance of *Homo sapiens* (Kloot 1991).

The terminology used when discussing biological invasions reflects various approaches and disciplines. Figure 1.1 shows symbolically the overlap of approaches. An invader may either succeed or fail to establish self-sustaining populations in areas of natural or near-natural vegetation or habitat (i.e. in original or modified ecosystems).

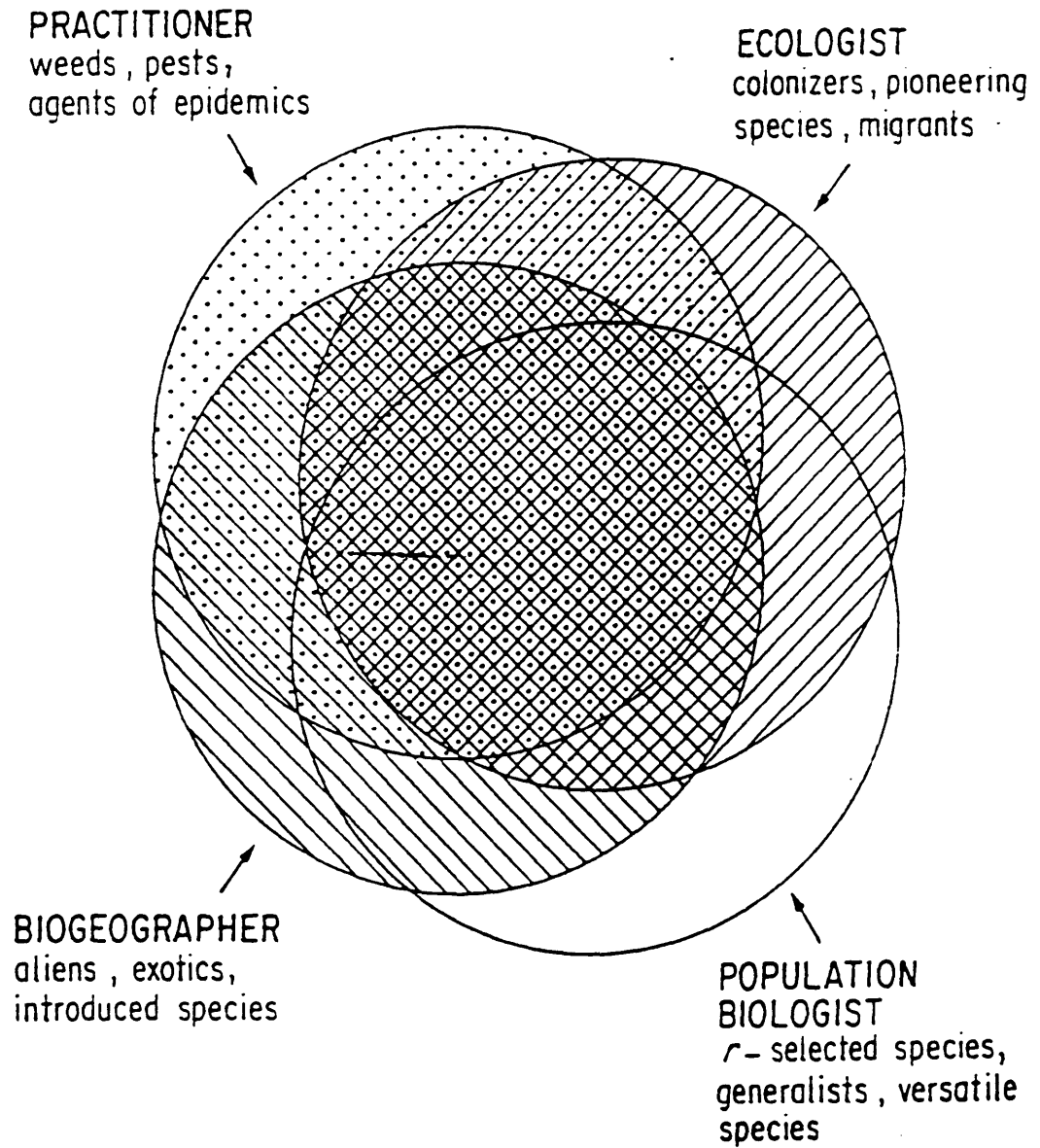


Figure 1.1 The symbolic overlapping and intercrossing of four approaches to cover the definition and characteristics of a biological invader. From di Castri (1990, 5).

Plant invaders that are successful are sometimes referred to as **naturalised** or established aliens. A naturalised species can be regarded as a species that has become established in an area and has reproduced for several generations in the wild (Wace 1978, Humphries *et al.* 1991). This definition has some problems when dealing with long-lived perennials such as shrubs and trees where insufficient time has elapsed for the passage of several generations.

A more useful approach was suggested by Smith (1988). He regarded woody plants in the process of naturalization as those which have populations outside their native range that include a large proportion of young individuals, not solely restricted to the immediate vicinity of parental individuals, and that receive little or no human assistance.

Naturalised species differ widely in their tendency to spread. The establishment of a self-sustaining population is the minimum criterion for an alien species to be regarded as a successful invader. The term **invasive** more generally denotes those species most evidently successful in spreading unaided into often disturbed ecosystems. Usher (1986) suggested that an invasive species is one that has become a pest and requires management to control population size or spread. Implicit here is a subjective judgement that an invasive species reduces the value of an area in terms of wildlife conservation value. A gradient of less-invasive to highly-invasive exists for all successful invaders. An organism that has spread little from its original site of introduction and require little

management would be regarded as less-invasive, while an organism that spreads far and rapidly from its point of introduction and requires costly management would be regarded as highly invasive.

Dictionary definitions of invasions usually have military connotations which suggest sudden, often violent incursions by aggressors into a new area. This approach is generally unsuitable for biological invasions, even though it has been used in the past (Elton 1958, Clark 1949). Invasions may occur over a span of days, months, years, or decades. Some works stipulate that an invading organism must have come from another country, and separate these invasions from those where organisms move within a country. Kookaburras (*Dacelo novaeguineae*) introduced from eastern Australia to Western Australia (Newsome and Noble 1986) and spread of Cootamundra Wattle (*Acacia baileyana*) within eastern Australia (Groves 1986a) are examples of 'internal' invasions. To assign political constraints to biological processes is impractical and has no sound reasoning (excepting island countries with strict quarantine regulations where checks supposedly can be made on invasions across borders).

A useful description of a biological invasion is to think of an organism that extends the range occupied by its population. This view is purposefully broad as it encompasses range expansion by individuals and propagules with and/or without human assistance. This removes the political/human connotation and concentrates solely on the organism. Range expansion may

occur by an individual or individuals arriving and remaining at a new location. This applies to all types of organism and encompasses different temporal and spatial scales. This also introduces similarities between invading and successional species (Lepart and Debussche 1991).

Groves (1986b) outlined the stages of a successful invasion. Successful invasions are characterized by **introduction** of the species which **colonizes** its new habitat by replication and after several generations, becomes **naturalised**. This is similar to Williamson and Brown's (1986) terminology of **arrival, establishment, and spread**. Indeed the term arrival is more objective than introduction which suggests humans acting as external agents of translocation. Many plants will inconspicuously and innocuously achieve the status of a successfully introduced species in any particular place, while others will be obvious and may become noxious.

Implicit in the colonization and naturalization phases is the process of range expansion. The rate at which species expand their range may be used to describe the invasiveness of plants (Roughgarden 1986). Other objective measures of invasiveness include the number of new individuals (implicitly measuring the rate of population growth), density of introduced organisms and areal extent of an invading population. For the purposes of this project invasiveness is measured by the rate of linear spread of the invading population.



In a practical sense most invasions by organisms have been helped in one way or another by humans (Kloot 1991). The most common help is through introducing an organism to a new environment. Organisms may be introduced intentionally for cultural and commercial reasons or accidentally as contaminants (Kloot 1991). Intentional introductions of agriculturally and horticulturally important plants have been well documented (Michael 1981, Kloot 1987). Aesthetic plants (many garden ornamentals) are an important group of introduced plants that are perhaps more insidious (Fox 1990) than other, and sometimes more spectacular, deliberate introductions such as prickly pear *Opuntia* spp. (Harper 1977) and Boneseed *Chrysanthemoides monilifera* (Weiss and Milton 1984).

#### 1.1.2 Characteristics of biological invasions with reference to Australia.

Biological invasions are a global phenomenon. They occur throughout time and space. di Castri (1989) traced trends in biological invasions and related them to periods of Earth and human history (see Tables 1.1, 1.2).

Biological invasions occur over Geological time scales whereby invasions by species from one continent to another are an integral part of the evolution of natural ecosystems. In general all large scale climatic changes and geological crises are at the origin of massive exchanges of flora and fauna from one biogeographic realm to another (see also Kloot 1991).

Pre-historical times saw the emergence of humans associated with synchronous climatic and tectonic changes which resulted in an increase in biological invasions. This is sometimes referred to as the Neolithic phase.

Historical times up to 1500 AD were characterized by stronger more extended human-made perturbations. Migrations and 'shaking up' of human populations within a given biogeographic realm meant exchange of biotic material. Improved marine transportation systems promoted the breakdown of biogeographic realms by humans. This period was the time of 'Great Discoveries' and European colonization.

The period from 1500 AD to the present witnessed the opening of new human routes across biogeographical realms. Intercontinental human migration and colonization were propelled by strong economic and social pressures made possible by new transportation and communication systems. This was the age of globalization and an 'acceleration' of time scale.

The present is characterized by the globalization of economies and markets. Urbanization, agricultural simplification, deforestation, lowering of biological diversity, new types of disturbance, genetic engineering, and human modification of climates are all modern phenomena.

Over longer periods, in geological time, biological invasions have contributed to the development of the unique Australian

biota. Gondwanic elements present in Australia 50 million years ago were the precursors of the modern flora and natural invasions augmented this southern heritage.

Table 1.1 Scale of biological invasions as regards the place of origin in a given invasion (from di Castri 1989).

migration distance (km)	Origin of invasion
0.01 - 0.05	From an individual to another group of individuals of the same or different species
0.1 - 0.5	From a different successional stage within the same ecosystem
10 - 10 <sup>2</sup>	From a different ecosystem type within the same region
10 <sup>2</sup> - 10 <sup>3</sup>	From a different region within the same biogeographical realm
10 <sup>3</sup> - 10 <sup>4</sup>	From a different biogeographical realm

Table 1.2. Scale of time of biological invasions with respect to the initial driving forces for a biological invasion (from di Castri 1989).

Time of occurrence of invasion (years)	Driving force of invasion
$10^4 - 10^7$ BP	Geological times characterized by natural disturbance ( e.g. climatic change associated with global glaciation) and new opportunities for migration associated with continental movements.
$10^3 - 10^4$ BP	Historical times characterized by direct and indirect human activities (primeval agriculture, nomadism).
1500 AD	Time of "Great Discoveries" and the breakdown of biogeographical realms. European colonization and immigration lead to introduction of edible and ornamental species.
1950	Increase world wide Urbanization and expansion of rapid transportation systems.
1970	Globalization of trade, markets and economies.
1990	Release by humans of newly genetically designed organisms.
2030	Human induced global climate change causing massive migration of whole biotas.

Prior to European settlement, Australian ecosystems had developed and were modified by Aboriginals over a period of at least 40,000 years (Kershaw 1986). Aboriginal settlement was regarded as having a relatively low impact on native ecosystems. Extensive burning practices, guided by cultural and spiritual beliefs, undoubtedly modified some Australian vegetation and animal communities (Gill et al. 1981, Kershaw 1986).

The advent of European settlement of Australia was seen as "an apocalyptic event for Australian ecosystems" (Adamson and Fox 1982). The impact of European settlement has encompassed modification of existing habitats and creation of new and different habitats (Fox and Adamson 1986). The British colonists in 1788 "brought with them a Noah's ark of animals and a botanical garden of plants" (Fox and Adamson 1986, 236).

In Australia the last three of di Castri's (1989) phases have all been compressed into the period since 1788. The modification of the Australian environment has proceeded at a rapid pace. Hobbs and Hopkins (1990) suggested that the 10,000 year or so history of agricultural development that has taken place in Europe and the Mediterranean, and allowed components of those ecosystems to develop with human technologies, has been confined to a mere 200 years in Australia with no parallel response from Australian ecosystems (see Fig 1.2). Biological invasions have therefore occurred over the past two centuries at a rate more rapid, and at times generally more recent, than in other continents. Their progress and

consequences therefore have generally not moved as far as in other places, making Australia an ideal 'natural laboratory' for their study.

Kloot (1991) recognized two processes of plant invasion in Australia. The first is invasion by 'naturally acquired' species over the past 70 million years or so corresponding to di Castri's geological period. This is principally through seed dispersal of self-fertile plant species transported by migrating birds flying between northern hemisphere wetlands and similar habitats in the southern hemisphere. Despite relatively rare events, the extensive time period combined with large numbers of birds making these flights must have resulted in a number of successful introductions.

The second process is that of intentional and accidental introduction of new plant species by humans. The first recorded example of a human-facilitated introduction of a plant to Australia was that of *Tamarindus indica* brought by Macassan fishermen for food (Macknight 1976). These people visited northern Australia from about 1700 to 1900, camping on the beaches and fishing in Australia's near shore waters for trepang (*beche-de-mer*).

This human phase of biological invasions was more rapid. In South Australia over 900 species of higher plant are now naturalised in a period less than 200 years, compared to about 60 naturally acquired species over millions of years (Kloot 1991).

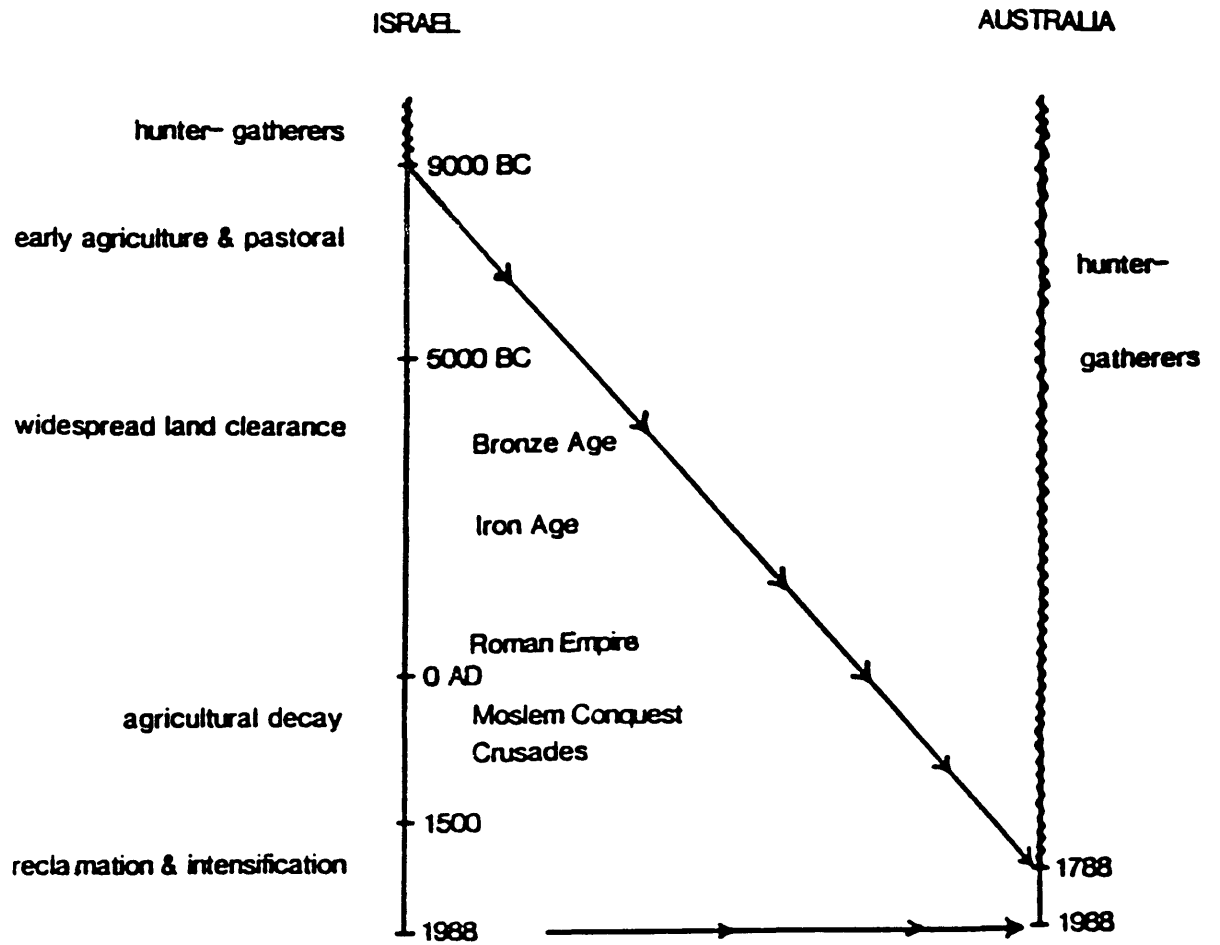


Figure 1.2 The modification of Australian ecosystems has taken place at a much faster rate than ecosystems in Europe and the Mediterranean. This figure shows symbolically the compression of human technology developed over thousands of years into 200 years in Australia (Hobbs and Hopkins 1990).

The geographical source of invading plants reflects the agricultural and economic history of a region (Shaughnessy 1986). For Australia its history is essentially European. Kloot (1991) presented data for South Australia and regarded this data as "at least indicative of that prevailing over the entire region of southern Australia with a mediterranean-type climate". Kloot compared the proportion of South Australian flora recorded as naturalised at three different periods (1855, 1909 and 1984). Some significant trends are apparent (see Table 1.3).

Table 1.3 The origins of the naturalized flora of South Australia at three different periods (from Kloot 1991).

Origin	1855		1909		1984	
	No. of species	(%)	No. of species	(%)	No. of species	(%)
Mediterranean	25	25	128	32	284	31
Europe <sup>1</sup>	50	49	142	35	232	26
Eurasia <sup>1</sup>	9	9	28	7	41	5
Asia	-	-	2	+	11	1
Eastern Asia	-	-	-	-	11	1
Old world tropics	-	-	3	+	8	+
California	2	2	2	+	8	+
North America	2	2	9	2	51	6
Central America	1	1	4	+	19	2
South America	4	4	18	5	63	7
South Africa	8	8	49	12	132	15
East Africa	-	-	1	+	9	1
Western Australia	-	-	1	+	5	+
South Australia	-	-	3	+	5	+
Eastern Australia and New Zealand	-	-	4	+	15	2
Garden origin	-	-	3	+	10	1
Totals	<u>101</u>	<u>100</u>	<u>397</u>	<u>100</u>	<u>904</u>	<u>100</u>

+ less than 1 per cent of total

<sup>1</sup> excluding that area immediately preceding in the list.



In 1855, a large proportion of the naturalised South Australian flora originated in Europe outside the Mediterranean Basin, or Eurasia. Only a small proportion of species were from the Mediterranean Basin and South Africa. By 1909 the proportion of species from Europe and Eurasia had fallen and that from the Mediterranean was increasing. This trend is even more marked by 1984. The proportion from South Africa remained relatively consistent over the time period. The proportion from America rose with South America increasing in importance.

This pattern is readily explained by immigration and trade patterns over the same period (Kloot 1991). Southern Australia was settled predominantly by northern Europeans. Many of the introduced plants from the earliest times of settlement were from these areas.

Introduction of South African plants was facilitated by ships from Europe stopping over in South African ports on the way to Australia, prior to the opening of the Suez Canal. A similar process operated via South American ports with plants making their way to Australia, first by a return trip to European ports, and then to Australia, probably as cargo contaminants (Kloot 1991).

The low proportion of North American species probably reflects the absence of regular and direct links between there and South Australia. Most of the North American species naturalised in Australia are also found in Europe and probably

made their way to Australia from there (Kloot 1991). However the gold rushes of the mid-1800s may have facilitated some introductions from North America (Fox 1990).

Approximately 10% of Australia's flora has been recently naturalized (Amor and Piggin 1977). This has probably increased. The proportion of naturalized flora also varies with location. In Sydney and Victoria the naturalized flora accounts for between 25%-33% (Heywood 1989).

The rate of naturalization of introduced species in South Australia averaged 6.1 species per year between 1802 and 1984 (Kloot 1991). This compares to 6 species per year for Victoria (Ross 1976) and 5.4 species per year for Western Australia (Kloot 1991). There is nothing to suggest that this rate is likely to reduce substantially in the near to mid-future (Groves 1991).

### 1.1.3 Ornamental plant invasions in Australia

Fox (1990), in analyzing plant invasions in regions with mediterranean-type climate i.e. parts of the Mediterranean Basin, California, central Chile, southern Africa and south western and southern Australia, recognized three phases of plant invasions related to human activities. Primary invasions coincided with the colonial and agrarian expansion of Europe. The second phase was characterized by invasions, principally by woody ornamental plants, particularly those with fleshy

fruits originating from southern Europe and the Mediterranean. The third phase involved invasions within each region of mediterranean-type climate of native species in response to human disturbance. Weir (1977) and Fox (1990) both see the long-term future of biological invasions leading towards a reduction in agrestal weeds and an increase in 'community' weeds, especially woody ornamental plants of Fox's (1990) second phase.

The results of the first and second phases of invasion was the focus of extensive research by Kloot (1991). He estimated that 57% of all naturalised plants in South Australia were introduced intentionally. The largest group of these were ornamentals which comprised 70% of all intentional introductions and 40% of the total naturalised flora (Table 1.4).

Of particular importance to this thesis was the invasion in Australia of fleshy-fruited ornamental species. They were introduced intentionally in many instances to both 'beautify' the Australian landscape and encourage birds into urban areas (Pizzey 1988, Mulvaney 1986).

Table 1.4. The manner of introduction of the naturalized species of South Australia. From Kloot (1991).

Intentionally introduced			
	Documented	Suspected	Total
Ornamentals	319	40	359
Fodder plants	58	17	75
Culinary plants	43	1	44
Hedges	14	-	14
Medicinals	8	5	13
Other	9	1	10
Total	451	64	515
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Unintentionally introduced			
	Confirmed	Possible	Total
Attached to stock	4	88	92
Contaminated seed	16	41	57
Ballast plants	7	36	43
Contaminated footwear	-	11	11
Contaminated fodder	3	3	6
Others	-	-	-
Total	35	179	214
No information			175
Grand total			904

These intentionally introduced ornamentals were likely to experience higher rates of establishment success, both from repeated introductions (Groves 1986a, Shaughnessy 1986), and from tending by humans (Kruger et al. 1986, Shaughnessy 1986) in the many and increasing number of gardens (Pizzey 1988). This differs from Baker's (1986) suggestion that ornamentals "have little hope of naturalization as weeds" principally because he regarded them as less robust and less able to survive in new environments than agricultural weeds adapted to extensive and intensive disturbance regimes. This divergence in thinking exemplified by Baker (1986) and Kruger et al. (1986) is more probably a reflection of the different agrarian (practitioner) versus environmental (ecologist, biogeographer) perceptions of biological invasions highlighted by Fig. 1.1, than any real difference between ornamental and agrarian weeds.

#### 1.1.4 Impacts of invasive plants

Invading plants have a variety of impacts on ecosystems (Mooney and Drake 1989). These include alteration of geomorphological process (e.g. *Ammophila arenaria* modified sand dune morphology in California and *Casuarina equisetifolia* increased sediment accumulation in Florida everglades (Macdonald et al. 1989)); alteration of biogeochemical cycling e.g. *Myrica faya* elevated nitrogen levels on young lava flows on Hawaii (Vitousek and Walker 1989), *Gunnera tinctoria* in Ireland (Osborne et al. 1991); alteration of hydrological

cycles (e.g. *Hakea sericea*, *Pinus pinaster*, *Acacia longifolia* and *A.mearnsii* reduced streamflows in South Africa (Macdonald and Richardson (1986)); alteration of fire regimes (Macdonald *et al.* 1989); and prevention of recruitment of native species (e.g. *Cytisus scoparius* preventing eucalypt regeneration in Australia (Waterhouse 1988)).

Some ramifications of these kinds of impacts include changes in faunal abundances (Braithwaite *et al.* 1989, Brown *et al.* 1991), local and global extinctions (Macdonald *et al.* 1989) and trophic cascades where introduced species indirectly affect a species which itself is directly unaffected by introduced species (Macdonald *et al.* 1989).

Fleshy fruiting ornamentals which become naturalized have importance extending beyond their competition with native flora. In Australia, which has relatively few fleshy fruited species in much of its vegetation (French 1991), they are likely to promote a range of impacts on native fauna. The fruit are ingested by a range of both native and introduced birds and the seeds subsequently dispersed into surrounding areas (Mulvaney 1986, Buchanan 1989, Bass 1990). Fleshy-fruited species commonly dispersed in this way include Large-leafed Privet (*Ligustrum lucidum*), Small leafed Privet (*L.sinense*), Firethorn (*Pyracantha* spp.) and Hawthorn (*Crataegus monogyna*) (Mulvaney 1986, Fox and Adamson 1986, Buchanan 1989, Bass 1990).

One strongly suspected impact of invading fleshy-fruited ornamentals in Australia is an increase in the over-winter

survival of Pied Currawongs (Recher and Lim 1990) which are also notorious nest robbers during spring and early summer (Frith 1976, Simpson and Day 1984). H.Recher (*pers comm.* 1990) has suggested that small bird species like Fairy-wrens (*Malurus*) and Thornbills (*Acanthiza*) may suffer increased predation by Pied Currawongs and consequently face local extinction, with consequences for other elements in their ecosystems. Similar fears exist in South Africa (Chown 1989).

Wells et al. (1986, 33) makes the poignant statement:

Since the imports were made to establish industries and gardens, the problems associated with today's plant invaders can be seen as a tax being paid by the community for the prosperity and amenities that have been and are still being enjoyed.

#### 1.1.5 Focus of biological invasion research

Studies of biological invasions have for the most part concentrated on characterizing the attributes of and situations concerning the invasion by successful invaders. While this has been rewarding, it has resulted in few robust generalizations. These generalizations fall into two principle categories; plant centred which searches for an invasive syndrome, and environment centred which characterizes invaded environments (Roy 1990). Roy (1990) suggested the need for a third, mixed approach to biological invasion research which

concentrates on the ecological interaction of an invader with the recipient environment.

Research of biological invasions has moved from documentation and anecdotal coverage (e.g. Ridley 1930, Elton 1958, Kitching 1986) towards a plethora of deeper investigations. These include dispersal ecologies (e.g. Murray 1986, Estrada and Fleming 1986), habitat and ecological modification (e.g. Vitousek and Walker 1989, Vitousek 1990, Lonsdale 1988, Lonsdale *et al.* 1989), population dynamics (e.g. Caswell 1982, 1989) and biological control of pest species (e.g. Cullen and Delfosse 1990).

In Australia much research of biological invasions has concentrated on agriculturally important annual and short-lived perennials (Michael 1981, Heap 1990). Recently more attention has been directed towards environmentally important species such as *Mimosa pigra* (Lonsdale *et al.* 1989), *Cytisus scoparius* (Waterhouse 1988), and *Chrysanthemoides monilifera* (Weiss 1986, Weiss and Noble 1984). See Humphries *et al.* (1991) for extensive treatment of other plant invasions and incidences of environmental weeds.

Attempts to answer the question 'What factors determine the success or otherwise of an invader?' have endeavoured to provide generalizations. Unfortunately many of these have been based on incomplete data (Newsome and Noble 1986). For example 14 of the first 18 species listed in *The World's Worst Weeds* (Holm *et al.* 1977) are C<sub>4</sub> species. Noble (1989) suggested that



this is more likely a reflection of the compiler's bias on the tropics which have a higher incidence of C<sub>4</sub> species. The success of an invader is a trade-off between inherent biological characteristics of the invader, abiotic and biotic factors of the source environment of the invader, and the invaded environment.

Groves (1986a) suggested that study of comparisons of an invasive species with a closely related but relatively less invasive species may prove fruitful. This was echoed by di Castri (1989,27) "More experimental research is needed particularly to understand not only why some species have been so successful as invaders, but also why closely related species are not invaders". This approach forms the conceptual framework of the present project. What makes one organism more invasive than another? In other words what controls invasiveness? Broadly we can look for clues in the following areas: attributes of the invader, attributes of the invaded environment, and relationships between the invader and other biotic components of the invaded environment.

#### 1.1.6 Attributes of biological invaders

Roy (1990) compiled a list (Table 1.5) of attributes of an invader from a range of previous works including Baker (1965) and Barrett and Richardson (1986). As with Baker's characteristics of an ideal weed, it is unlikely that a successful invader will have all the characteristics in the list, nor is an invader necessarily likely to succeed if it

has any of the characteristics. Newsome and Noble (1986) suggested that most introduced plants tend to be 'specialists' with particular requirements for germination and relatively poor plasticity rather than being super-generalists. These plants take advantage of particular situations exploiting suitable opportunities for invasion.

Table 1.5. Characteristics of the 'ideal' invader (from Roy 1990).

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*Physiology*

Germination requirements fulfilled in many environments.  
 Discontinuous germination through induced dormancy.  
 Great longevity of seeds.  
 Rapid growth due to fast resource acquisition rate.  
 High material allocation flexibility.  
 Broad physiological response breadth.  
 High acclimation potential.  
 High ability to compete with other species.

*Demography*

High population growth rate.  
 Early reproductive maturity.  
 High reproductive output.  
 Reproduction over a wide range of environmental conditions.  
 Long temporal and spatial dispersal of seeds.

*Genetics*

Self-compatibility; if not, wind pollinated, or unspecialized floral structure with pollination by generalist.  
 Not obligatory self-pollinated so as to allow for ecotypic differentiation.  
 High flexibility of the genetic systems allowing modifications of recombination rates.  
 Apomixis or vigorous vegetative reproduction if perennial.  
 High genetic variation.  
 Polyploidy.

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Lepart and Debussche (1991) however suggested that for a limited set of characteristics there is little difference between successional species and invaders. Kloot (1991), based on the early naturalised flora of South Australia, noted that invaders were more likely to possess a 'general purpose' genotype than be specialists. Again this divergence in the characteristics of invaders stems from the difference of approaches of researchers and analysis of incomplete data sets (Newsome and Noble 1986). Table 1.5 reflects a predominantly agrarian view of weeds and largely disregards ornamental plants (see section 1.1.3 and Fig. 1.1).

#### 1.1.7 Attributes of invaded environments

Much of invasion success depends upon abiotic and biotic similarities of the source and invaded environments (Holdgate 1986, Newsome and Noble 1986). Indeed preadaptation of an invader to a new environment is seen as a distinct benefit and precursor to successful invasion (Kruger *et al.* 1986). Of particular note is the similarity between climates of source and invaded environments. Climate is a major barrier that an invader must overcome if it is to succeed in its new environment (Swincer 1986). It then follows that when source and invaded environments have similar climates an invader is likely to be more successful (but see Kruger *et al.* 1986 for South African examples). Roy *et al.* (1991) challenged the idea of homoclines as a means for predicting success of an invasion. They found the width of tolerated climate a better predictor of invasion success. Species with a wide home range

will have a better chance of success in a new environment (as long as there is some overlap in climate between the two areas). This supports the generalist strategy of invading plants suggested by Kloot (1991).

Factors other than climate have also been implicated in determining invasion success. *Hakea sericea*, an Australian species invading areas in South Africa, is limited there by the presence and absence of quartzite- and sandstone-derived soils (Kruger et al. 1986). Fire, often a disturbance factor promoting invasions, may exclude some invasions through reduction of recruitment at fire-sensitive stages (Groves 1986a). Rolls (1981) described the interplay of a changed fire and grazing regime in the reinvasion by local native shrubs in the Pilliga region of north western New South Wales.

Biotic factors also play a major role in determining invasion success. Escape from predators and pathogens may enhance survival and recruitment of invaders at particular stages in the life cycle. The net result would be an increased rate of population growth and hence invasiveness. Availability of suitable pollinators and seed dispersers may also facilitate invasions.

The role of disturbance as an important precursor to biological invasions is generally accepted. Disturbance may be anything that kills or damages individuals within a given area, or affects resource levels within that area (Hobbs 1989, 1991). Fox and Fox (1986) state categorically that there is no

invasion of natural communities without disturbance. In invaded, apparently natural, communities there is always some degree of subtle alteration of disturbance regimes (Fox and Fox 1986). There tends to be greater invasion with more prolonged, repeated or more intense disturbance. However the long history of extensive disturbance in the Mediterranean Basin has resulted in a relatively invasion resistant flora (Lepart and Debussche 1991) which differs to other mediterranean-type regions with their shorter history of human agrarian disturbance regimes. Since European settlement, dramatic human modifications to natural disturbance regimes are likely to have precipitated acceleration of biological invasions in Australia (Hobbs 1991).

No single simple cause nor a few obvious characteristics can explain biological invasions (Newsome and Noble 1986). This is a function of the multiplicity of interpretations and extent of biological and edaphic factors (Lepart and Debussche 1991).

#### 1.1.8 Safe sites and biological invasions

Johnstone (1986) discussed the process of biological invasion in such a way as to avoid specific ecological situations and move towards a universal approach utilizing Harper's (1977) safe sites. Johnstone argued that no matter how fast a population grows or how many propagules it produces, "without a safe site, that reproductive productivity is meaningless and invasion is impossible" (Johnstone 1986, 375).

Johnstone (1986) proposed four categories, which are all time dependent (but are importantly not caused by time), and depend on the removal of barriers enabling an invader to have access to a safe site. These categories, termed windows, are default, temporary, stable and future windows. With sufficient safe sites, the rate of invasion will be determined by the rate at which windows open (or rather barriers removed). Barriers may be biotic (e.g. other plants), abiotic (e.g. oceans), species-selective (selective to a given species not already present) or non-selective (a barrier to all species not present).

Default windows comprise situations where invasions cannot take place. An example is the non-invasion by photosynthetic plants into the permanent darkness of a cave. Temporary windows occur when an invasion takes place only when a temporary opportunity presents itself, often through the removal of a biotic barrier (e.g. a plant removed through disturbance). Stable windows present continued opportunities for invasion by a specific species once a barrier is overcome. This is often a physical barrier overcome by dispersal. A future window exists for a specific species in the future and is facilitated by removal of biotic or abiotic barrier (e.g. dormant seed or suppressed seedling released by gap creation).

Under this classification the invasion by fleshy fruiting ornamental plants in Australia could best be classified as a stable window invasion. In the first instance humans act as dispersal agents overcoming an ocean barrier. Once established, continued range expansion by the invader, which

could be interpreted as a series of separate smaller invasion events over shorter distances, could also be classed as a stable window invasion. In this instance, seed dispersal to new areas overcomes a barrier. Instinctively, the differences in the rate of invasion of fleshy fruiting ornamental species may be related to the rate at which stable windows open, or rather, the effectiveness of dispersal affected by humans and vertebrates, provided there are sufficient safe sites available.

## 1.2 The project.

*Crataegus monogyna* and *Prunus mahaleb* are two introduced plants that are in the process of naturalization on the Northern Tablelands of New South Wales. Both were previously members of the family Rosaceae (Tutin *et al.* 1968). *C.monogyna* is now placed in the family Malaceae and *P.mahaleb* in the related Amygdalaceae (Harden and Rodd 1990a,b). Both originate from Europe where they co-occur (Tutin *et al.* 1968). Both are deciduous trees that bear vertebrate-dispersed fruits. However, despite these similarities, they display markedly different relative invasiveness in eastern Australia.

Central to this thesis is the assumption that as both species' ranges overlap in their original and invaded environments, abiotic environmental factors have little influence on their degree of invasiveness. The differences in invasiveness in Australia are more likely explained by biological differences between the species, the ways in which each species behave in

Australia, and the influence of humans in the course of their respective invasions. This project seeks to address which of these factors are important in determining this difference.

From the range of factors which characterize successful invasions outlined in sections 1.1.6, 1.1.7 and 1.1.8, the following broad hypotheses are suggested and will be addressed in the thesis. (1) The role of humans in introducing and planting will influence the degree of invasiveness of a species (Chapter 3). (2) A more invasive species will have a higher rate of population growth than a less invasive species (Chapter 4). (3) A more invasive species will have more effective long-distance seed dispersal than a less invasive species (Chapter 5).

The project then is a comparative study of the relative invasiveness of two related introduced woody plants hawthorn (*Crataegus monogyna*) and St Lucie's Cherry (*Prunus mahaleb*) in the Armidale region. The project will concentrate on the histories of both species in Australia (Chapter 3), their demographics (Chapter 4), and dispersal ecologies (Chapter 5) with the goal of explaining why hawthorn has invaded rapidly and widely, to the point of becoming locally noxious, in striking contrast to St Lucie's Cherry which has invaded only a small area within the same region.



### 1.3 Study region

The study region is centred around the township of Armidale (30:30S 151:39E) (latitude-degree:minutes South, longitude-degrees:minutes East) on the Northern Tablelands of New South Wales (see Fig. 1.3). Armidale is a major regional centre with a population of *c.* 23 000. It is a major provider of secondary and tertiary education as well as a centre for meat and wool production.

The Northern Tablelands is a part of the much larger eastern highlands, a discontinuous plateau extending from northern Queensland to Victoria in the south. The eastern highlands were formed by broad tectonic uplift prior to the Pliocene and linked to tectonic activity associated with the opening of the Tasman-Coral sea initiated by sea floor spreading (Ollier 1986).

The Northern Tablelands region is characterized by low relief, being mostly flat with many lagoons and swamps characteristic of internal drainage. The tablelands lay astride the topographic divide separating the westward flowing rivers (e.g. the Gwydir River) from the numerous eastward flowing rivers before they descend the Great Escarpment (Ollier 1986). Much of the tablelands are above 1000 m in elevation with some local higher peaks (e.g. Mt Duval, see Fig. 1.3).

Details of climate for the Armidale district are from Smith (1990) and weather summaries by Burr (1988-1992). There is a

marked graduation in precipitation across the tablelands. Precipitation is at a maximum of approximately 2000 mm at the top of the Great Escarpment and decreases inland to the west. Winds are generally westerly in winter and spring and turn more easterly in summer. The average annual rainfall at Armidale is 789 mm with a summer maximum attributed to convective rainfall (Smith 1990).

Table 1.6 shows the yearly precipitation totals seven years prior to and during the duration of data collection of this project. Of note is the drought years of 1981 and 1982 and the relatively dry year of 1986. Rainfall was near average during most of the project except for 1990 with 924 mm (Burr 1988-1992).

Table 1.6 Yearly rainfall totals in millimetres between 1980 and 1991 for Armidale, New South Wales (from Burr 1988-1992).

Year	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	MEAN
Year													
total	515.8	653.0	460.2	914.2	893.4	756.8	506.6	785.6	722.0	765.6	924.2	728.4	787.6

The yearly averages hide considerable variation in seasonal totals. The summer of 1988-1989 was exceedingly dry with the November-February four month total of 220.8 mm, 38% below the mean of 356.1 mm. The same period of 1989-1990 recorded above average rainfall of 481.4 mm.

Armidale has an average annual daily maximum and minimum temperature of 20.3 and 7.3 degrees Celsius. Armidale has an average of 70 frosts days per year and snow on *c.* 1 day a year. June, July and August are the coldest months with mean daily minimum temperatures below 5 degrees Celsius (see Table 1.7).

Table 1.7 Mean daily minimum and maximum temperature (degrees Celsius) for Armidale (from Burr 1988-1992).

	J	F	M	A	M	J	J	A	S	O	N	D	MEAN
Mean daily maximum	27.1	26.2	24.2	20.6	16.5	13.2	12.4	14.1	17.6	21.1	24.3	26.4	20.3
Mean daily minimum	13.7	13.5	11.5	7.6	4.0	1.8	0.6	1.3	3.7	7.2	10.0	12.4	7.3

#### 1.4 Study sites

Within the immediate study region centred on Armidale were two principal study sites. These were the Armidale State Forest (ASF site) and a section of a cattle and sheep grazing property 'Newby Park' (Saleyards site). A third site was located within the grounds of the University of New England (UNE site). The locations of all the sites appear on Fig. 1.3.

##### 1.4.1 Armidale State Forest (ASF)

The ASF site was located in the Armidale State Forest approximately 6 km north east of the township of Armidale. The

forest was gazetted on 14 July 1915 and now comprises an area of 247 ha (Forestry Commission of New South Wales 1982). The forest is dominated by duplex and rocky soils developed on sedimentary rocks, greywacke and claystones comprising the Sandon beds (Forestry Commission of New South Wales 1982).

Approximately 121 ha consists of exotic species, predominantly *Pinus radiata*. Other introduced trees include *P.muricata*, *P.torreyana*, *P.strobus*, *P.pinaster*, *P.ponderosa*, *P.canariensis*, and species of *Quercus*, *Fraxinus*, *Robinia* and *Populus*. Many of these plantings are concentrated in an arboretum near Commissioners Waters.

The Eucalypt dominated woodland vegetation was largely cleared for forestry operations. Some areas of remnant vegetation exist in the southern part of the forest. These remnants include *Eucalyptus blakelyi*, *E.dalrympleana*, *E.viminalis*, *E.nova-angelica*, *E.bridgesiana*, *E.melliadora*, *E.caliginosa*, and *Angophora floribunda* (Forestry Commission of New South Wales 1982). ASF has been invaded by numerous fleshy fruiting woody plants including *Crataegus monogyna*, *Prunus mahaleb*, *Ligustrum* spp., *Pyracantha* spp. and *Cotoneaster* spp.

The pre 1920 *Pinus* stands are the oldest surviving plantation grown trees in New South Wales and have both historical and scientific interest (Forestry Commission of New South Wales 1982). The plantation has changed its management focus from timber production towards the maintenance of recreation values. Consequently management activities are directed towards the removal and replacement of senescent trees and reduction of fire hazards.

Cattle graze the forest under licence. The benefits of this practice are the reduction of fire hazard and some control of noxious weeds (Forestry Commission of New South Wales 1982).

A number of study plots were located within compartments 1-6 in the western side of the forest (see Fig. 1.3). This section of the forest contains pre 1920 *Pinus*. Subsequent plantings of *P.radiata* c. 10 years of age in the immediate vicinity were designed to replace old and senescent trees.

The first plot, ASF1 has an area of 1.2 ha and is orientated approximately north-south. Two other plots, ASF2 and ASF3, are each 10 m<sup>2</sup> and located 30 m east of ASF1. ASF2 and ASF3 are located within a *P.mahaleb* thicket. Numerous 1 m<sup>2</sup> and 25 m<sup>2</sup> plots were located near ASF1 to monitor seedlings (see Chapter 4 for more details).

#### 1.4.2 Saleyards site

The Saleyards site was located on a sheep and cattle grazing property 'Newby Park'. It was selected as *C.monogyna* forms a very dense understorey there characterized by several impenetrable thickets. 'Newby Park' is located approximately 4 km west of Armidale off the Bundarra Road (see Fig. 1.3).

The previously extensive eucalypt woodland has largely been cleared. Some large *E.viminalis* and *A.floribunda* trees remain on the steeper and rocky slopes. As mentioned the understorey

is dominated by *C.monogyna* shrubs with occasional *Rubus fruticosus*.

Two plots, Saleyards 1 and Saleyards 2, 200 m<sup>2</sup> and 225 m<sup>2</sup> respectively, were orientated north-south down a south facing slope. Numerous 1 m<sup>2</sup> quadrats were located within and adjacent to the main plots (see Chapter 4).

'Newby Park' has been used for wool and meat production for over 50 years (R. Vyner *Pers comm.* 1988). The thickets of *C.monogyna*, while restricting access to some parts of the immediate paddock, provide valuable shelter for stock against cold southerly and westerly winds (R. Vyner *pers comm.* 1988)

#### 1.4.3 University of New England site (UNE)

The University of New England main campus is located approximately 4 km north west of Armidale (see Fig. 1.3). In the northern part of the campus is a basalt-capped hill dominated by *E.viminalis* and *A.floribunda*. The area was once grazed by domestic stock but is now only grazed by native macropods (Wallaroes and Kangaroos) and the introduced rabbit. Located throughout the area are numerous *C.monogyna* shrubs along with many plants of *Cotoneaster*, *Pyracantha*, *Rubus fruticosus* and *Ligustrum*.

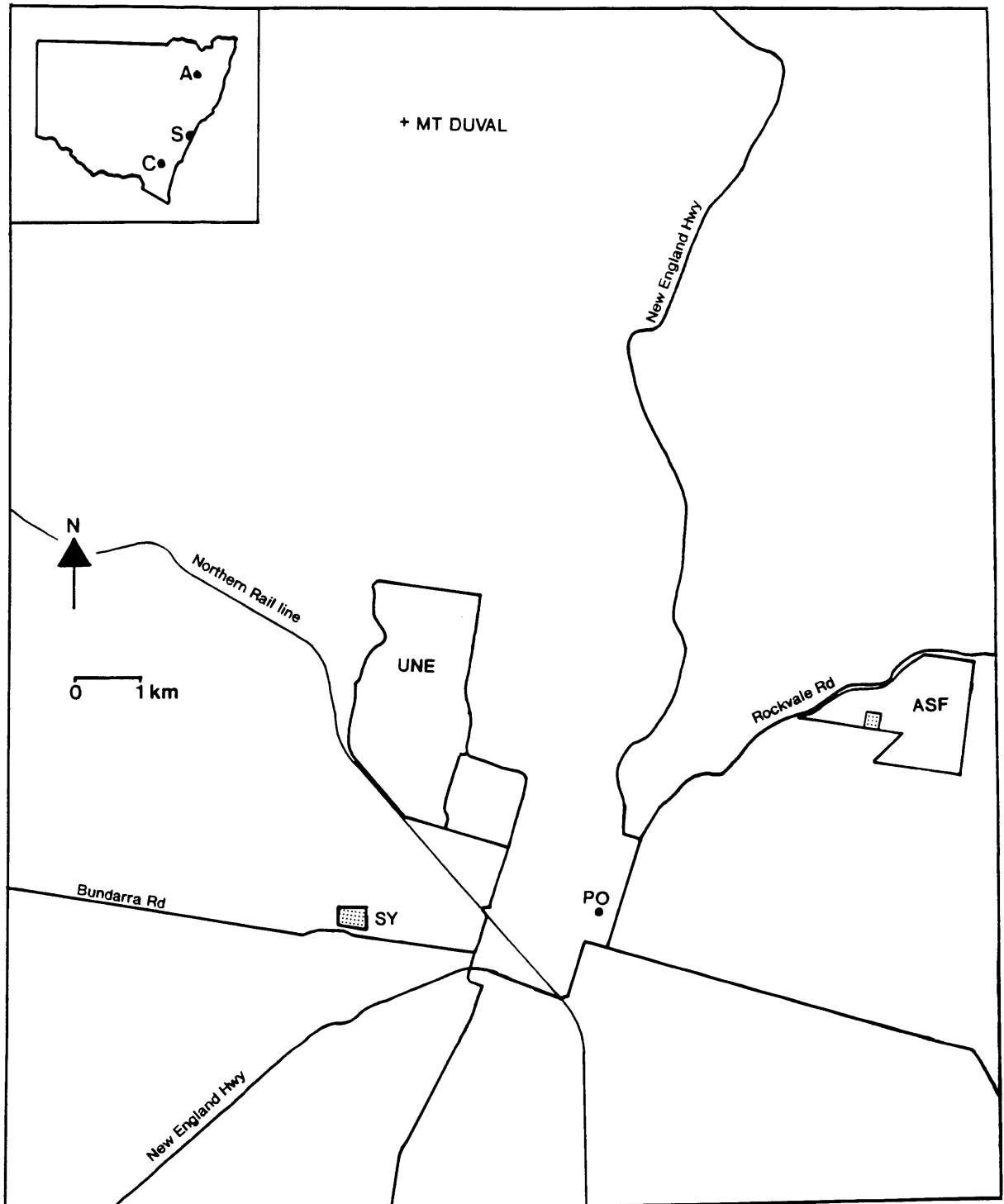


Figure 1.3 The location of study sites near Armidale, New South Wales. ASF = Armidale State Forest, SY = Saleyards site, UNE = University of New England, PO = Post Office. Shaded boxes represent the location of study plots at each site. Inset shows location of Armidale (A), Sydney (S) and Canberra (C) in New South Wales.

CHAPTER 2: MORPHOLOGY, PHENOLOGY, REPRODUCTIVE ECOLOGY AND DISTRIBUTION OF CRATAEGUS MONOGYNA AND PRUNUS MAHALEB.

Plant names follow Harden (1990) who uses the taxonomic scheme of Dahlgren (1980). Thus the family Rosaceae is divided into a number of smaller families.

2.1 *Crataegus monogyna*

*Crataegus monogyna*, previously of the family Rosaceae (Tutin *et al.* 1968) now included in the Malaceae (Harden and Rodd 1990a), is a member of the large genus *Crataegus* L. comprising deciduous, usually spiny shrubs or small trees. *C.monogyna* is commonly known as Hawthorn. Other names include May, Mayblossom, Quick, Thorn, Whitethorn, Haw, Ladies' Meat and Bread and Cheese Tree (Leyel 1976, Addison 1985). Hawthorn is widespread in the British Isles where it was planted as live "quick" hedges, and from where it was brought to Australia.

Hawthorn is steeped in history and mythology. It has been variously reported that hawthorn was used for Christ's crown of thorns (Leyel 1976), the Glastonbury thorn produced from the staff of Joseph of Arimathaea (Addison 1985), and that the wizard Merlin of King Arthur's court was trapped in a whitethorn tree (Campbell 1948). The smell of hawthorn flowers is also said to be reminiscent of the smell of the Great Plague of London (Leyel 1976).



### 2.1.1 Uses of *Crataegus monogyna*

As well as the mystical and spiritual side of hawthorn it has a number of medicinal purposes. Its bark contains the alkaloid Crataegin and like other members of the *Prunus* and *Pyrus* groups of the Rosaceae contains Amygdalin. Hawthorn has been used as a diuretic and cardiac tonic. A tincture made from hawthorn reportedly effectively lowers systolic and diastolic blood pressure (Abdul-Ghani et al. 1987). Trace elements including Cr, Cd, Pb, Cu, Mn, and Zn were extracted from fruits and flowers and were considered by Kiseleva, Samylina, Baratova et al. (1989) as promising sources of trace elements for the treatment of trace element metabolism in cardiovascular disease. Other cardiovascular and pharmacological uses for hawthorn include an anti-arrhythmogenic agent (Costa et al. 1986), a source of flavonoids, procyanides and alkylamines and amino acids and a source of vitamin C (Farkas 1987, Kiseleva, Samylina, Orolova et al. 1989).

Additionally hawthorn fruit can be added to brandy to produce a distinct liqueur. Hawthorn wood is dense and is considered to burn with a great deal of heat, so much so that charcoal made from hawthorn wood was used to melt pig-iron (Leyel 1976). Hawthorn has also been used as grafting stock for other *Crataegus* species and some closely related fruits (Lombard 1989).

By far the most common use of hawthorn and indeed its reason for introduction into Australia was as a hedge plant. The trees were commonly planted in a hill-ditch arrangement. After a few years growth the hedge was cut and layered to promote vigorous and dense growth (see section 3.2.1 for description of management of hedges). In this way hawthorn hedges provided relatively cheap fencing. As well, the hedges also provided cover for foxes and game birds which were hunted for sport (Ridley 1930). Von Mueller (1895) recommended hawthorn as one of the most eligible among deciduous hedge plants for introduction into Australia. He expounded the quality of wood for engraving and recommended the flowers for honey production.

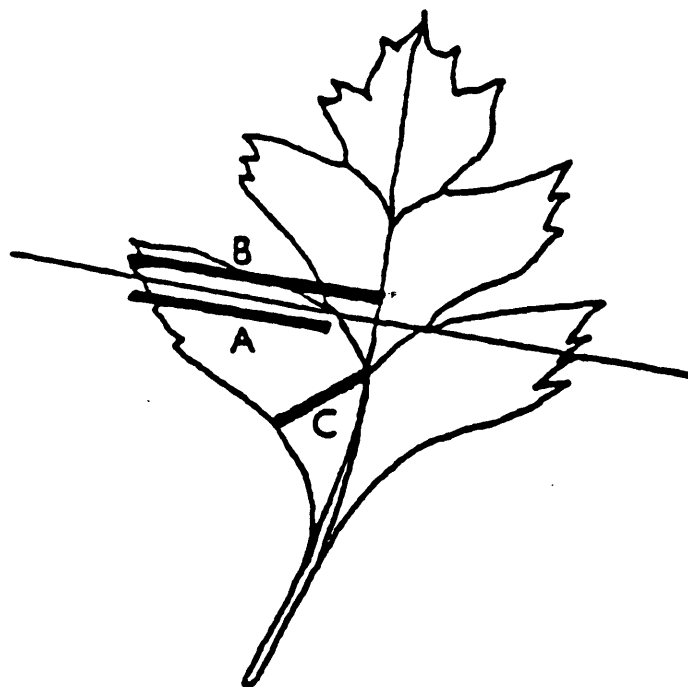
#### 2.1.2 Taxonomy

There are around 200 species of *Crataegus* throughout temperate regions of the world, especially the Northern Hemisphere. In North America a great deal of debate and confusion over the limits of species has centred on *Crataegus*. Brown (1910) detailed the divergent thinking of systematic botanists. Certainly *Crataegus* species very readily hybridize and this has led to a proliferation of sub species and variants.

Of relevance to this project is *Crataegus monogyna*, often also referred to as *C.oxycantha*. *C.monogyna* is a variable species and the taxa associated with *C.monogyna* have been treated by various authors (see do Amaral Franco 1968). In Europe, *C.monogyna* hybridizes readily with *C.laevigata* and other

species (Byatt 1975). As part of the present study material collected in Australia was analysed using the methodology of Byatt (1975). The ratios of lowest lateral sinus depth to half leaf width (A/B) and lowest leaf-lobe width to half leaf width (C/B) were calculated (see Fig. 2.1). The ratios were multiplied by 100. South-east English material were found by Byatt (1975) to fall along a gradient from pure *C.monogyna* to pure *C.laevigata*. *C.monogyna* had a A/B ratio of c. 70 with a minimum and maximum of c. 63 and 91 respectively. Material collected from plants growing in the grounds of UNE (sample of 100 leaves - ten leaves from ten individuals) had a mean A/B ratio of  $63 \pm 8.9$  (range 41.3 to 82). The C/B ratio from English material is c. 40 (range 29 to 49) while UNE samples had a mean of  $37 \pm 8.9$  (range 18 to 59).

This suggests that the Australian material is slightly more variable than true *C.monogyna*. Many plants around Armidale have pink tinges to their petals. Together with a 1.05% incidence of two fruit stones per fruit (N = 502 fruit) this suggests that there is some degree of hybridization or at least some variability in *C.monogyna* in New England. Photocopies of specimens from Tasmania and the Central Tablelands of NSW were likewise analysed for leaf morphology. These data are shown with English and Armidale material in Table 2.1. Plants in UNE were less deeply lobed than UK material and suggest some intergrading towards the *C.laevigata* form. As Byatt (1975) suggested despite being a variable species most hybrids tend towards the *C.monogyna* form. This is a function of the abundance of *C.monogyna* which makes for



- A = Lowest lateral sinus depth.**  
**B = Half leaf width.**  
**C = Lowest leaf-lobe width.**

Figure 2.1 The morphology of a *C.monogyna* leaf and the measurements used to generate leaf and sinus depth ratios. From Byatt (1975).

higher incidence of backcrossing with this parent.

Table 2.1. Leaf morphology of *C.monogyna* in Australia and south-eastern England (after Byatt 1975). Sample sizes are shown in brackets.

Locality	Mean $\pm$ sd	Min.	Max.
(a) A/B ratio			
UNE	63.02 $\pm$ 8.93 (100)	41.34	81.98
C. NSW	69.2 $\pm$ 11.69 (20)	45.95	100.19
Tasmania	69.57 $\pm$ 9.65 (15)	55.39	85.13
England <sup>1</sup>	70	63	91
(b) C/B ratio			
UNE	36.98 $\pm$ 8.93 (100)	18.02	58.66
C. NSW	46.29 $\pm$ 10.41 (20)	29.79	68.34
Tasmania	44.88 $\pm$ 8.01 (15)	26.67	58.93
England <sup>1</sup>	40	29	49

<sup>1</sup> Figures shown for South-eastern England are estimated from figure 4 in Byatt (1975). As such the exact means and ranges are not known.

### 2.1.3 Morphology

*Crataegus monogyna* Jacq. *Fl. Austr.* 3:50 (1775) (*C.oxyacantha* L., nom. ambig.) is a shrub or small tree growing to 10 m. The branches and trunk are armed with spines 7-30 mm long. The leaves are ovate, 1-4.5 cm long with 3-5 deep lobes, and are entirely or sparsely toothed near the apex. The sinuses are usually deep with the lowest lateral sinus extending at least

2/3 to the midrib. Flowers are arranged in umbel-like corymbs. There are five sepals and petals with the petals usually white. There is a single style with a deep red pome fruit 8-12 mm diameter containing a single boney carpel. A small proportion, c. 1% of fruit contain two carpels and are likely an artefact of internal natural variation or a result of hybridization with some relatively less common ornamental varieties.

#### 2.1.4 Phenology

In New South Wales *Crataegus monogyna* sheds leaves in autumn, from the end of March through to April. New leaves appear around the second week in September. Flowering occurs over a two week period in mid-October. Fruit are initiated in late October and ripen in early autumn (March) and remain on the tree until October. Some fruit remain until the following summer by which time they are usually severely degraded, becoming dehydrated and woody. Seeds germinate over one month, from the second week in September to mid-October. Shoots grow from September through to autumn, finishing prior to leaf fall.

Figure 2.2 summarizes the phenology of *C.monogyna* near Armidale. The phenological timetable generally shifts in the order of two to three weeks with changes in altitude and latitude. Phenological stages are two to three weeks later for populations in the southern highlands of NSW than those around Armidale (personal observations).

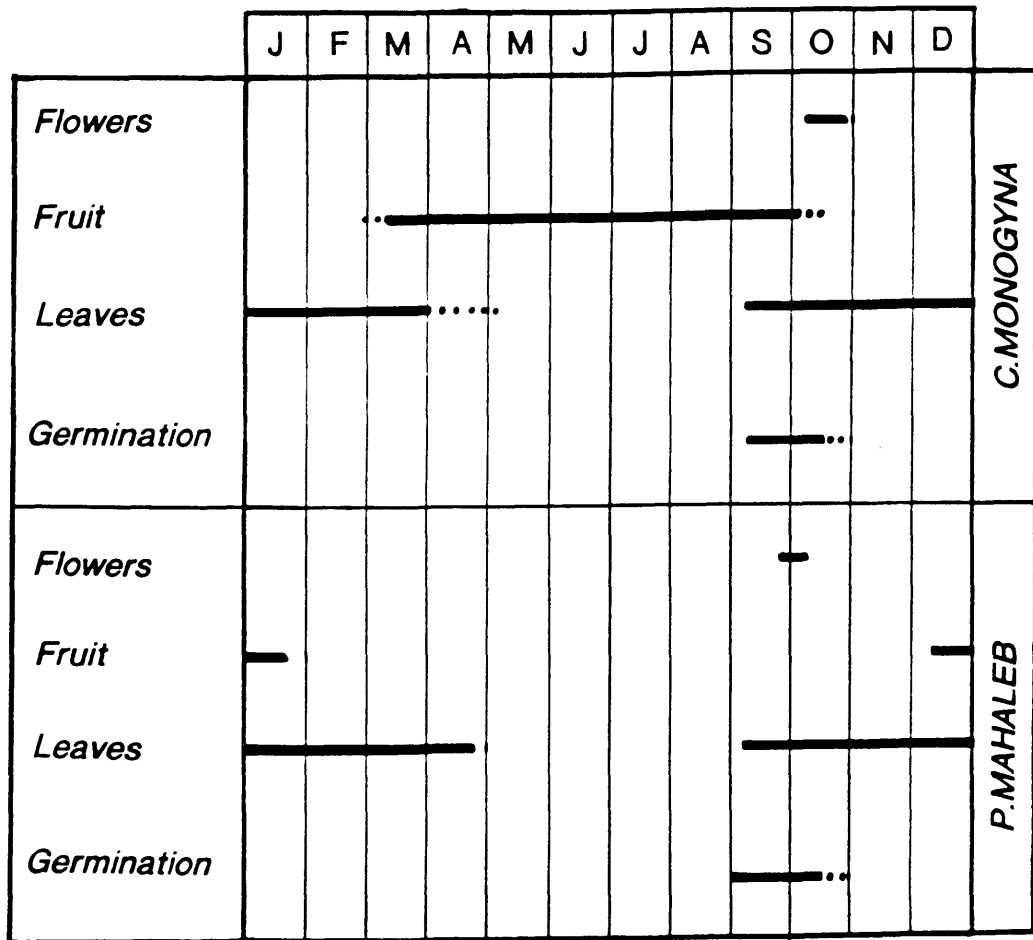


Figure 2.2 Phenological timetable of *C.monogyna* and *P.mahaleb* at Armidale, New South Wales.

### 2.1.5 Reproductive ecology

*Crataegus monogyna* produces insect pollinated white flowers that occur in clusters of 10-15 on corymb-like structures. A wide range of insects were observed at the time of flowering. These included flies, introduced honey bees, soldier beetles and ants. Apomixis has been reported in some members of *Crataegus* (Campbell and Dickinson 1990) but is unknown in Australia. *C.monogyna* may resprout and sucker from roots and basal stems after cutting and disturbance (Shoard 1980). The seed dispersal ecology of *C.monogyna* is dealt with in detail in Chapter 5.

### 2.1.6 Distribution

*C.monogyna* is widespread throughout Europe (de Amaral Franco 1968). In Australia *C.monogyna* tends to be restricted to the cooler and higher localities. *C.monogyna* is common on the Northern, Central and Southern Tablelands of New South Wales, in northern and central Victoria, around the Adelaide Hills and in Tasmania (Harden and Rodd 1990a, personal observations, herbaria records). It is a common hedge and ornamental plant and now has become naturalised in agricultural and semi-urban areas.

The distribution of *C.monogyna* in New South Wales, established by correspondence with state herbaria, Weeds Officers in the New South Wales Department of Agriculture and Fisheries and by personal observations while driving through country New South Wales, extends from near the Queensland border to Nimmatabel



in the south east of New South Wales (see Fig. 2.3). Smith (1982) mapped the extent of *C.monogyna* along roadsides on the Northern Tablelands (see Fig. 3.2). *C.monogyna* generally grows above 800 m with the majority of populations above 900 m. The distribution of *C.monogyna* is more or less continuous along the tablelands. There are discrete populations centred on Tenterfield in the north (discussed in detail in Chapter 3) and Tingha in the north west. This separation may be a function of planting of hedges, availability of suitable sites for establishment, or rate of spread. In years to come these two separate populations may coalesce with *C.monogyna* in the rest of the region.

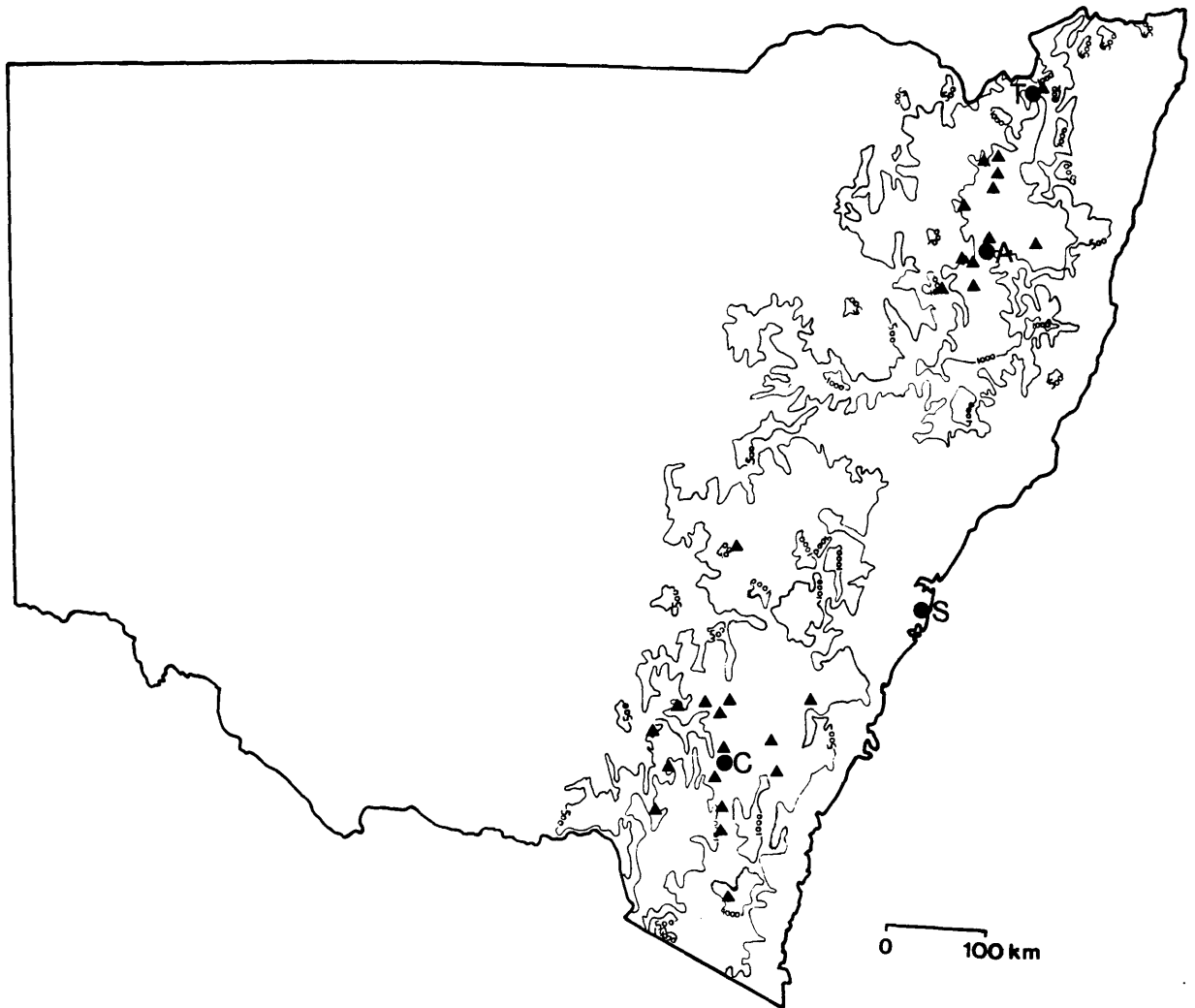


Figure 2.3 Distribution of *C.monogyna* in New South Wales identified from herbaria records, correspondence with New South Wales Department of Agriculture and Fisheries Weeds Officers, and from personal observations as of 1993. T = Tenterfield, A = Armidale, S = Sydney, C = Canberra. The 500 m and 1000 m contours are shown.

## 2.2 *Prunus mahaleb*

*Prunus mahaleb*, previously in the large family Rosaceae (Tutin *et al.* 1968) is now included in the Amygdalaceae (Harden and Rodd 1990b) and is commonly known as St. Lucie's Cherry. It is native to central and southern Europe (Webb 1968) and occurs as a small and expanding population centred on the Armidale State Forest, northeast of Armidale, New South Wales (Smith 1988). It was probably first introduced to Australia as a hardy rootstock for commercial fruit trees. *P.mahaleb* is a popular rootstock for sweet cherries (Johnson 1985) for a variety of reasons. These include drought tolerance due to deep rooting and minimal surface rooting, production of medium sized and highly productive precocious trees, suited to light sandy and gravelly soils, tolerant of calcareous and alkaline soils, tolerance to bacterial canker, and earlier maturation of fruit (Menzies 1990, Westwood 1978). Von Mueller (1895) recommended *P.mahaleb* for introduction into Australia as a source of scented seeds for making maraschino liqueur, and for odorous wood for turning pipes and other articles. The flowers could also be used for perfumes.

### 2.2.1 Taxonomy

Approximately 430 species of *Prunus* occur throughout north temperate and tropical regions (Harden and Rodd 1990b). Some native species of *Prunus* occur in New Guinea and northern Australia (Smith 1988). All species in New South Wales have been introduced (Smith 1988). A range of *Prunus* species are

already or are becoming naturalized in New South Wales. These species are shown in Table 2.2.

Table 2.2. *Prunus* species naturalized or becoming naturalized in New South Wales (from Smith 1988).

<i>P.persica</i>	Peach and Nectarine
<i>P.armeniaca</i>	Apricot
<i>P.domestica</i>	European Plum
<i>P.salicina</i>	Japanese Plum
<i>P.avium</i>	Sweet Cherry
<i>P.dulcis</i>	Almond
<i>P.cerasifera</i>	Cherry Plum
<i>P.cerasus</i>	Sour Cherry
<i>P.laurocerasus</i>	Cherry Laurel
<i>P.lusitanica</i>	Portuguese Laurel
<i>P.serotina</i>	Black Cherry
<i>P.mahaleb</i>	St Lucie's Cherry

Most *Prunus* species are taxonomically distinct. However *P.cerasifera*, *P.domestica* and *P.salicina* occur with possible hybrids (Smith 1988). This is due in the main to *Prunus* species' importance as fruit trees and development of a range of varieties and hybrids suitable for different locations. There is therefore some degree of difficulty in assigning specific and varietal names. Despite this *P.mahaleb* does not appear to have hybridized with any other *Prunus* species in the Armidale area.

### 2.2.2 Morphology

*Prunus mahaleb* L., *Sp. Pl.* 474 (1753) (*Cerasus mahaleb* (L.) Miller) is a shrub or small tree growing to 6.0 m and displaying a spreading habit. Young twigs are

characteristically glandular to puberulent. Leaves are 4-5 cm long and are broadly ovate, cuspidate, with a round to subcordate base. The leaf margins are crenate or more serrate with conspicuous marginal glands. They are glabrous, or slightly pubescent beneath. The flowers are fragrant and borne in short corymbose racemes of 3-15 flowers. These corymbose racemes terminate short, lateral leafy shoots. The pedicels are c. 10mm and have campanulate hypanthium. Petals are white and 5-8 mm long. Fruit are ovoid to spherical and range from 8 to 10 mm in diameter. They ripen from green to red to black and have a thin mesocarp which is bitter to taste. The fruit contains one large seed in a smooth endocarp (Smith 1988, Webb 1968).

### 2.2.3 Phenology

*Prunus mahaleb* sheds leaves in Autumn. New leaves appear in about the second week of September. Flowering occurs over a two week period at the end of October. Fruit are initiated in early November and ripen during December. All fruit disappear by mid February. Seeds germinate between the beginning of September and mid-October. Shoots grow from September through until Autumn, finishing prior to leaf fall. Figure 2.2 shows the phenology of *P.mahaleb* in comparison with *C.monogyna* at Armidale.

#### 2.2.4 Reproductive ecology

*Prunus mahaleb* produces insect pollinated white flowers in clusters of 3-15. A wide range of insects were observed at the time of flowering. These included flies, introduced honeybees, soldier beetles and ants and were the same species as those observed on *C.monogyna*. *Pmahaleb* may resprout from the base after felling of trees. The seeds also display dormancy which is broken by stratification (Ellis et al. 1985).

#### 2.2.5 Distribution

*P.mahaleb* occurs throughout Central and Southern Europe and extends through to Ukraine in the east and Belgium in the north (Webb 1968). It has become naturalized in eastern North America (Phillips 1978). In Australia *P.mahaleb* is restricted to a small population centred on the Armidale State Forest. The main population occurs within the forest. Some individuals occur in neighbouring properties to the South and West of the main population (see Fig. 2.4).

As *P.mahaleb* is an important horticultural species, research has been undertaken to assess the characteristics of the species in numerous fruit growing regions in Australia. As a result *P.mahaleb* has been planted and used for rootstock in Southern Queensland, Northern, Central and Southern Tablelands of New South Wales, Northern and Central Victoria, and the Adelaide Hills. It is not known whether *P.mahaleb* has 'escaped' from these areas but is a distinct possibility through abandonment of orchards and ready availability of fruit trees through commercial nurseries.

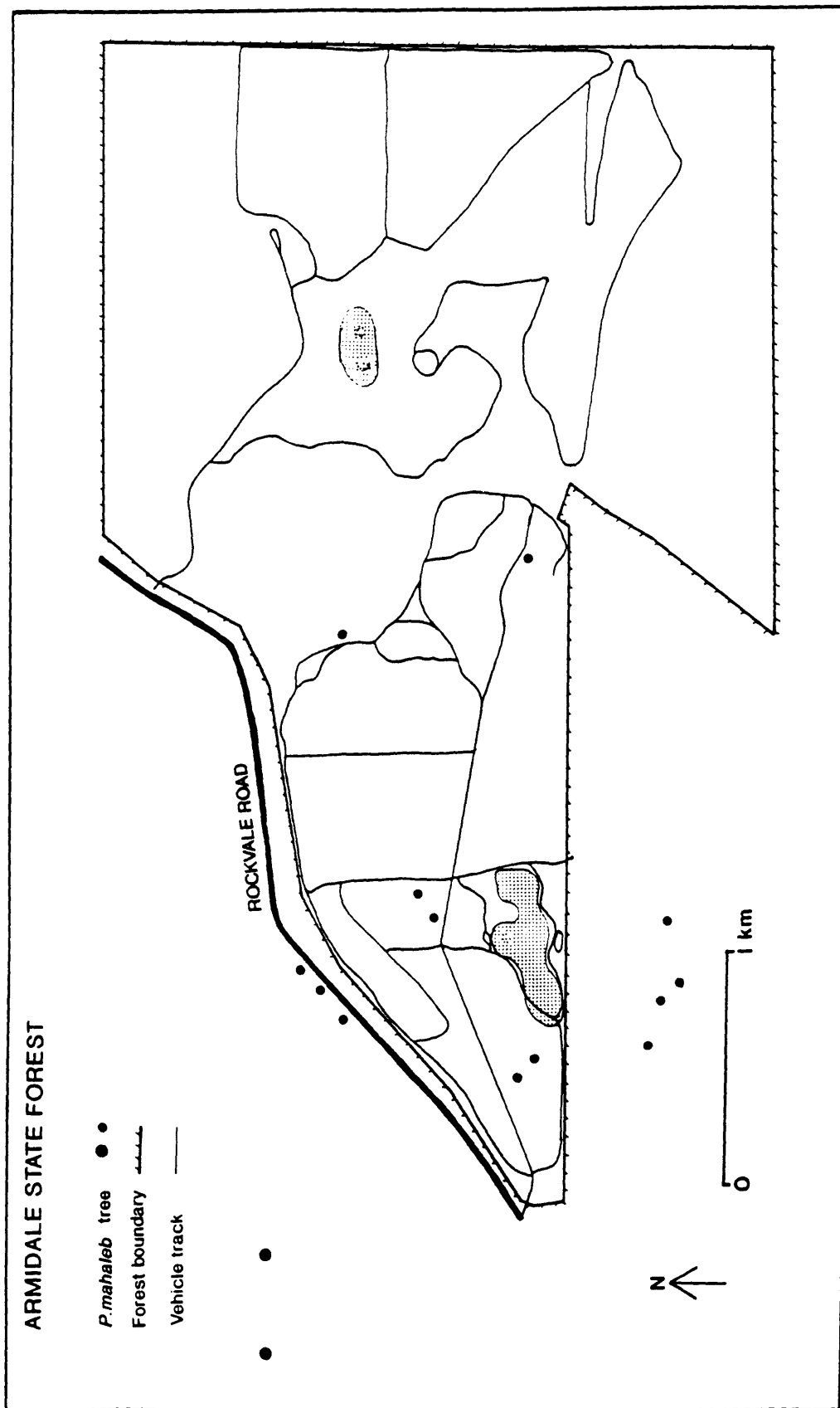


Figure 2.4 Distribution of *P. mahaleb* around the Armidale State Forest, 1994. Stippled areas represent dense thickets.

CHAPTER 3: HISTORY OF *CRATAEGUS MONOGYNA* AND *PRUNUS MAHALEB*  
IN AUSTRALIA AND THEIR RATES OF SPREAD

The role of humans in biological invasions was briefly dealt with in Chapter 1. The major facets of human influence include the initial, and often repeated (Michael 1981, Groves 1986a), introduction of an organism to a new area, the tending of that organism, especially ornamental plants, in order to ensure its survival, and then the dispersal of the species beyond its site of introduction.

The introduction of woody plants, and particularly ornamental plants, is likely to be intentional (Kloot 1991). Seeds are usually large and therefore accidental introduction (e.g. by contamination) is unlikely. *C.monogyna* and *P.mahaleb* both have aesthetic and economic value and it was for these reasons that both were intentionally introduced to Australia. The course of their invasions are therefore likely to be inextricably linked to the actions of humans. Two case studies are used to describe the history of both species in the region. The treatment of *C.monogyna* centres on the isolated population of the plant around the township of Tenterfield. By necessity the treatment of *P.mahaleb* is confined to the Armidale region.

### 3.1 The process of range expansion

The process of spread of a biological invader is clearly described by Roughgarden (1986) and is best visualized by



following the population growth and range expansion of a hypothetical population introduced to a point on a uniform plane. As the individuals in the population disperse and colonize new areas, the population's range expands. An individual can disperse in any direction with equal probability and dispersal distances are normally distributed. Exponential population growth takes place at every place the population reaches. If a line is drawn through all points with a given population density then the radius of the circle increases linearly with time.

In the real world the environment is not uniform and the pattern of population density contours is not circular. Where the range of a population is not circular, a better relationship exists between the square root of the area occupied and time. This approach, pioneered by Skellam (1951), still oversimplifies patterns seen in nature. Mack (1985) and Moody and Mack (1988) recognized that many invaders do not advance along a radiating front but rather radiate from multiple, disjunct foci. These foci may differ in size because of their different dates of establishment. Therefore most invasions are characterized by one or a few large foci at the point of introduction and many more and perhaps less obvious smaller foci (satellites) at some distance away from the point of introduction. If the initial area of a single large focus and the initial combined area of many small satellite foci are the same, and all foci grow at the same rate, the satellite foci will collectively occupy space much faster than the

single large focus (Mack 1985, Moody and Mack 1988, see Fig. 3.1).

In a practical sense small foci will have more reproductively mature individuals near a population boundary than will a single large focus. This situation would lead to more propagules arriving in previously unoccupied sites from small foci, compared to more propagules landing within the existing population of a large focus (Mack 1985, Moody and Mack 1988). This exemplifies the important link between range expansion and propagule dispersal (Bazzaz 1986 and Noble 1989).

From a theoretical perspective control measures directed at biological invaders should, under a wide variety of circumstances, be directed to the inherently more important satellite foci. Mack and Moody (1988) cite examples of weed control strategies which target satellite foci in North America (common barbery - *Berberis vulgaris*) and South Africa (*Hakea sericea* and *H.gibbosa*).

#### 3.1.1 Rates of spread

The rate of spread of various tree taxa in the British Isles during the Holocene have been estimated by Birks (1989) from palynological data representing 135 radiocarbon-dated sites. Isochrone maps join sites at which pollen-stratigraphical events occurred at the same time.

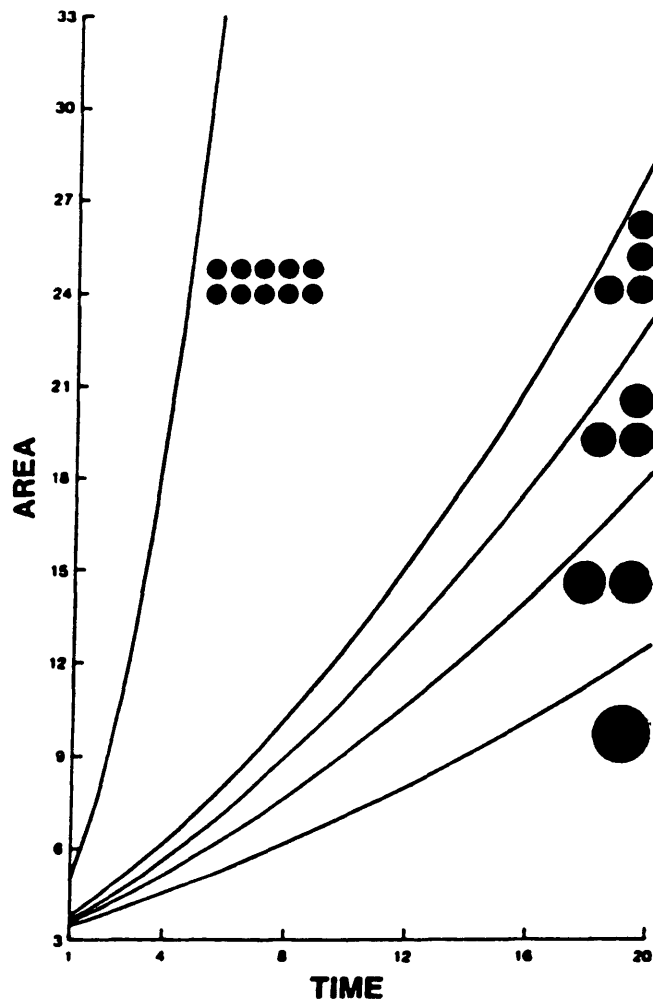


Figure 3.1 The addition of foci increases the rate of new range occupation in the form of a quadratic function even if the total area initially remains constant. In this example plotted from Mack (1985, 133) the area occupied by  $n = 1, 2, 3, 4$  and 10 foci at any one time  $t$  ( $1, 2, \dots, 20$ ). At  $t=0$  (not shown) each group of foci beside its curve has the same total area.

These events usually are the first identified rise in pollen abundance of a particular taxon. Rather than identifying an advancing front of a species, isochrone maps identify a threshold population density of trees where pollen production first becomes detectable by standard palynological techniques. The presence of populations at low densities ( $< 1 \text{ tree ha}^{-1}$ ) may remain unrecorded (Bennett 1986). There is a lag between arrival of first individuals (barely detectable palynologically) and the rise of the population densities to threshold levels whereby their presence can be identified by sustained local increases in pollen. If this lag time is assumed to be relatively constant over a wide geographical area then the rate of spread of the first expansion episodes can be regarded as representing the rate of spread of the first arrivals (Birks 1989). Table 3.1 shows the estimated rates of spread of woody taxa in the British Isles and Europe ranging from  $50 \text{ m yr}^{-1}$  for *Fraxinus* to  $>2000 \text{ m yr}^{-1}$  for *Betula*.

Table 3.1 Estimated rates of spread of trees in the British Isles and mainland Europe (from Table 1 in Birks (1989)).

Taxa	Rate of spread ( $\text{m yr}^{-1}$ )	
	British Isles	Mainland Europe
<i>Betula</i>	250	$>2000$
<i>Corylus</i>	500	1500
<i>Ulmus</i>	100-550	500-1000
<i>Quercus</i>	50-350-500	150-500
<i>Pinus</i>	$<100-700$	1500
<i>Alnus</i>	50-150-500-600	500-2000
<i>Tilia</i>	50-100-450-500	300-500
<i>Fraxinus</i>	50-200	200-500
<i>Fagus</i>	100-200	200-300

Birks (1989) found no consistent difference shown between taxa dispersed by vertebrates, wind or water. The relatively rapid rates of spread (those greater than  $500 \text{ m yr}^{-1}$ ) were likely the result of chance events rather than consistent and 'normal' dispersal (Birks 1989).

### 3.1.2 Determination of rates of spread

For presently invading trees, knowing the date of original introduction and age of daughter plants at various distances from the point of introduction, it is possible to calculate rates of spread. Aging of plants is possible for species that form annual growth rings corresponding to a dormant phase of growth (usually winter cold) juxtaposed with a period of rapid growth (usually spring and early summer).

Both *C.monogyna* and *P.mahaleb* are suitable for dendrochronological analysis as both species are deciduous and have well defined growing seasons (Baillie 1982). On inspection both species were found to produce well defined annual growth rings. For both species the same techniques were employed in order to determine plant ages. After felling trees with a chainsaw, a section of stem was taken as close to the ground as possible. In some instances uneven and rocky ground precluded a basal section. However all stem sections were generally taken less than 15 cm above ground level. The stem sections were then sanded with a belt sander using 80 grit paper. The smoothed sections were then coated with a dilute clear estapol varnish which made the contrast between spring

and summer wood more distinct. The annual rings were then counted from the outside towards the centre of the section. A ready check of ages could be made by the identification in older specimens of two narrow rings associated with the drought of 1980-1982 (see Chapter 1). For even older specimens a further narrow ring was associated with a drought in the region in 1965-1966 (Burr 1988-1992). Age estimation from counting annual growth rings only provide 'best estimates' which make allowances for missing rings, variation in sampling height above ground and variation in the rate of plant growth. to the height at which ring samples were taken (Ogden 1985).

### 3.2 *Crataegus monogyna* in Australia

Hawthorn was probably first introduced to Australia for two principal reasons. These were for use in hedges (Kloot 1986), and cultural and aesthetic reasons. It appears that the introduction of English plants and establishment of hedges was a high priority to the early settlers of New South Wales. Charles Darwin (1839 cited in Browne and Neve's 1989 edition of the *Voyage of the Beagle*, Mackaness 1965) remarked of his 1836 journey across the Blue Mountains west of Sydney along the Parramatta-Bathurst road "This line of road is the most frequented and has been the longest inhabited of any in the colony. The whole land is enclosed with high railings, for the farmers have not succeeded in rearing hedges". Another important use of hawthorn planted in hedges was as a wind break for orchards (Robert Miller *pers comm.* 1994). At Armidale, hedges of hawthorn marking the perimeter of the

property Palmerston, were planted in order to provide cover for foxes (*Vulpes vulpes*) which were hunted from horseback (J.M.B. Smith *pers comm.* 1993).

Hawthorn was a common and characteristic plant of Britain. Many of the early settlers to the New England Tablelands were of Celtic and Anglo-Saxon stock. It was only natural then that these settlers brought with them hawthorn as one of their most useful and familiar plants (*sensu* Kloot 1991, also see Chapter 1).

It is probable that most of the hawthorn that entered Australia came as seed as this would have been far easier to transport during the arduous trip by ship from Europe than seedlings. Once in Australia seed and seedlings would have become available through a variety of nurseries, probably located in Victoria and the central highlands of NSW which were more suited for propagation of hawthorn as compared to Sydney. Much of the orchard stock and garden supplies for Australia originally came from the Melbourne Botanic Gardens. The Botanic Gardens, under the direction of the State Botanist Ferdinand von Mueller, who became an office bearer (and Vice President in 1861) of the Acclimatization Society of Victoria, encouraged, propagated and sold an extensive array of introduced plants (Pizzey 1988, Von Mueller 1895).

Hawthorn has a wide distribution in New South Wales, being present in the Central and Southern Coast, and Southern, Central and Northern Tablelands (Harden and Rodd 1990a) (see

Fig. 2.3). The rate of spread of hawthorn can be estimated on a number of scales. *C.monogyna* extends from Nimmatabel (36:29S, 149:17E) on the southern Tablelands near the Victorian-New South Wales border (personal observation, 1993) right through to Wallangarra (28:54S, 151:56E) north of Tenterfield near the Queensland-New South Wales border (personal observation, 1990), a distance of approximately 900 km (see Fig. 2.3). This range has certainly been attained since initial European settlement in 1788, but more probably since the early part of the nineteenth century, when the Blue Mountains west of Sydney were successfully crossed after 1813 and the tablelands and western slopes were opened up to European settlement. This gives a very conservative date of introduction of hawthorn to inland Australia around 1815. The immediate area around Sydney would probably not have been suitable for the propagation of *C.monogyna* due to its higher average temperatures, bearing in mind that *C.monogyna* prefers cooler (usually higher elevations) areas to grow (see Fig. 2.3). In the early days of the settlement there was more interest in growing sufficient food to head off starvation than rearing ornamental hedge plants (Currey 1966, Hughes 1988). Certainly Charles Darwin saw no evidence of hawthorn in hedges (and reported no garden specimens) in 1836 when he travelled from Sydney to Bathurst via Parramatta (Browne and Neve 1989, Mackaness 1965). The rate of spread of *C.monogyna* (if Sydney is taken as the source of plants with first introduction of *C.monogyna* to the Central Tablelands and western slopes of New South Wales) is approximately 450 km in 175 years or just over 2.5 km yr<sup>-1</sup>. This of course would have been facilitated by



humans transporting plants and seeds to new pastoral settlements and townships. Of greater interest here is the apparent unaided (secondary ?) spread of *C.monogyna* away from original plantings.

The potential for hawthorn to spread away from hedges and into the surrounding paddocks was noted at the turn of the century. A transcript of a conversation in 1989 between Ruth Chant, a local historian, and Ms Rubie McIntyre, an elderly resident of Armidale and previously living near Ebor approximately 90 km east of Armidale (see Fig 3.2), illustrates the situation admirably:

**Ruth Chant:** Do you remember the hawthorn hedge?

**Rubie McIntyre:** By Jove do I!

**RC:**When was that planted, that hawthorn hedge?

**RM:**Oh, in Taylor's time, love - I'll be truthful- too old for me to remember. But we remembered it growing up like, and we were only kids.

**RC:**When were you born?... [I estimate around 1896]

**RM:**I remember that hawthorn. We had it at home, but dad never liked it so we never actually [had a hedge]. Put a tree in here and there, but we never watered...and finally they died except one. And it grew down near the wash room. Oh! they're a curse! I could never see the beauty in them, tell you the truth. They was thorny and all. They was sort of spiteful if you got near them. Hey hey! I don't like thorny things like that.

**RC:**Where did your dad get them from?

**RM:**Taylor's - in their time. He got the plants and put them in. And of course they grew like wildfire on the Guy Fawkes soil - and 'Bonnie Brook' too.

**S. Chant:**Where do you think Mr Taylor got them from?

**RM:**Well he was an Englishman, so I couldn't tell you that.

**SC:**He brought the seeds over?

**RM:**Well probably. I couldn't answer that one to be truthful, but they were planted in Taylor's time. We thought at first that they were nice, you know... But they grew, and they grew, and there was thorns and prickles everywhere, and we chopped ours out. I think we got one left.

**RC:**Dad chopped the ones out at 'Bonnie Brook' too.

**SC:**He cut down that big hedge because they were spreading in the paddock, you know.

**RM:**Oh, for miles! If you rode the paddocks at home like, and at Mr Chant's too, you'd see little fellers coming up. As old

Mr Turnbull said: "Get down off your horse and cut the brutes out!" [laughter] And he was wise. Formerly they had them. He never liked them.

**RC:** He got rid of them at Kotupna too, did he?

**RM:** Yeah, yeah.

### 3.2.1 Tenterfield case study

Tenterfield at an altitude of 850 m on the northern Tablelands of New South Wales (see Fig. 3.2) is a small township of some 3500 people. Tenterfield is approximately 190 km north of Armidale. It was settled in the early 1840s and some of the original properties still survive today. One characteristic of the area is its numerous hedges of *C.monogyna*. It is likely that many of these hedges date from the late 1800s and early 1900s. Many of them were planted for the purpose of enclosing stock and protecting orchards from cold winds. These types of hedge required regular maintenance to keep them stockproof. Traditional hedge management dictated that hedges had to be laid by hand every five years (Shoard 1980). Laying a hedge involved cutting off the tops of bushes and then the remaining stems were interwoven. The injury caused by cutting and layering promoted vigorous regrowth which became dense and closed holes in the hedge. This was labour intensive and with the advent of cheaper fencing materials the maintenance of hedges went out of fashion. In Britain mechanization and reduction in farm labour promoted a decline in the maintenance of hedgerows. It is likely that a similar fate befell hawthorn hedges in Australia. The situation today is that most hedges are in severe disrepair and have been kept stockproof with the

addition of fence wire and posts. Many of the hedges today still follow original fence lines and property boundaries.

Tenterfield lends itself to analysis of the rate of spread of *C.monogyna* as the population of *C.monogyna* is separate from the general background population of *C.monogyna* further south on the tablelands. This is shown on Fig. 3.2 adapted from Smith (1982). Figure 3.3 shows the distribution of hedges, major infestations of *C.monogyna* and individual trees that were aged by counting of annual growth rings.

'Tenterfield Station' was one of the original properties in the district and the economic centre of the district (TS in Fig. 3.3). The first legal title for 'Tenterfield Station' was granted in the name of R.R. Mackenzie in 1842. In 1844 Stuart Alexander Donaldson took over 'Tenterfield Station' in his own name under an annual lease. Donaldson was finally given full lease of 'Tenterfield Station' in 1848. Donaldson later became New South Wales' first Premier in 1856. 'Tenterfield Station's influence extended north to the Queensland border (Lloyd Woolnough *pers comm.* 1993). The station supported a large number of rural workers and supplied much of the agricultural and horticultural produce to the region's settlers.

'Tenterfield Station' was later broken up into smaller holdings. J.E. Summerlad purchased 'Spring Valley' and 'Leeches Gully' (see Fig. 3.3). 'Spring Valley' located near the intersection of Commercants Road and the Mount Lindesay Highway was the centre of extensive orchard plantings.

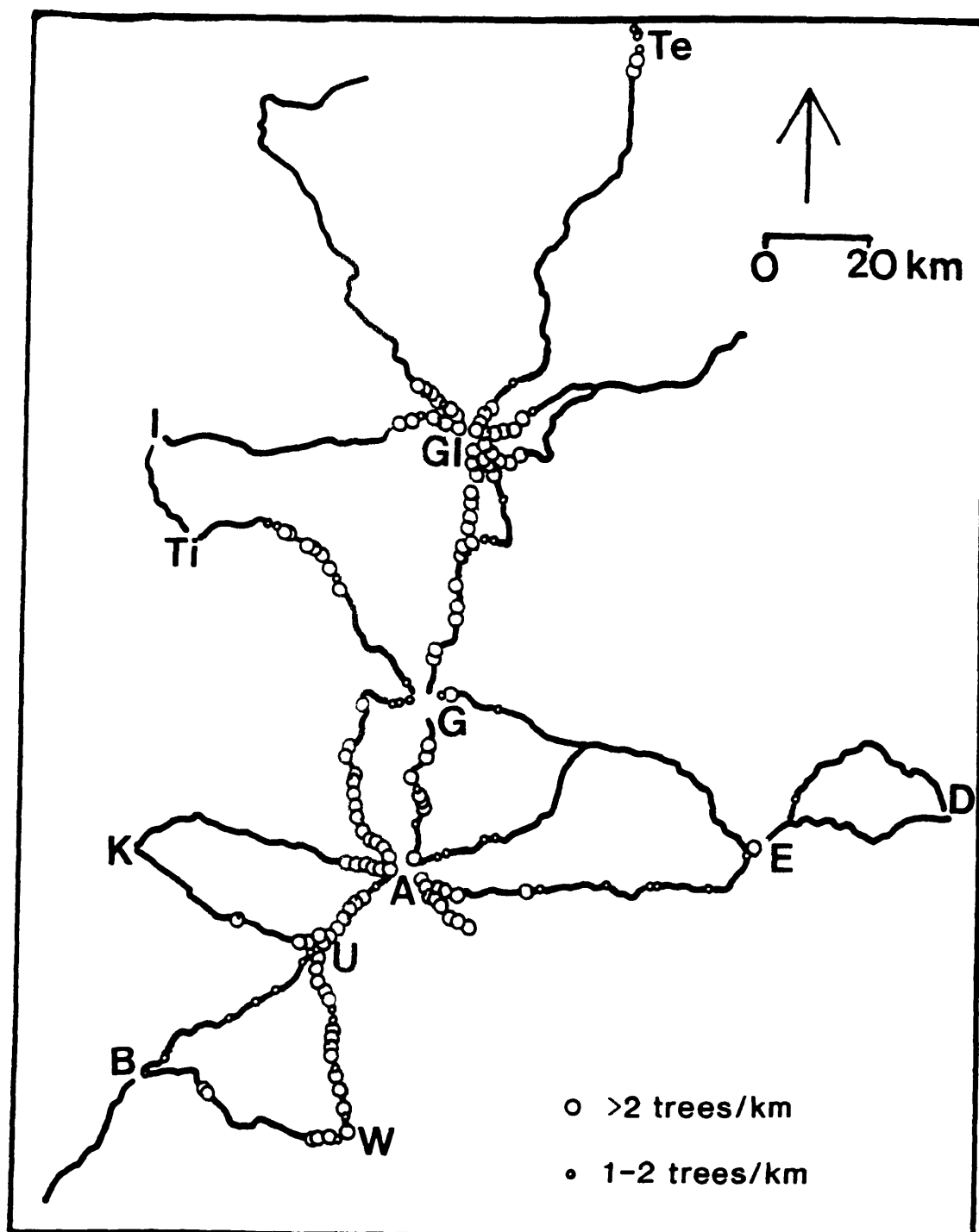


Figure 3.2 Distribution of *C. monogyna* along roadsides on the Northern Tablelands of New South Wales. Te = Tenterfield, GI = Glen Innes, I = Inverell, Ti = Tingha, G = Guyra, D = Dorrigo, E = Ebor, A = Armidale, K = Kingston, U = Uralla, B = Bendemeer, W = Walcha. Modified from Smith (1982).

Summerlad was a notable local Tenterfield settler responsible for setting up a dairy, butter factory, orchard and nursery in Tenterfield that supplied northern NSW and southern Queensland with produce. Situated not far from the main Summerlad house are a number of large hawthorn hedges and now a severe infestation of wild hawthorn.

Approximately 1 km south from 'Spring Valley' along Millers Road, 'Poplar Gardens' (now know as 'The Poplars'), the site of hedge A in Fig. 3.3, was owned by the Miller family. Robert Miller came to Tenterfield in the 1850s. He was employed on 'Tenterfield Station' where he was responsible for garden and orchard stock. In 1863 he took over 'Poplar Gardens' (L.Woolnough *pers comm.*1994). There Robert Miller established an orchard (Anon, 1894). Robert Miller was regarded as the founder of the fruit industry in Tenterfield (Anon 1894). In photographs supplied by Lloyd Woolnough, 'Poplar Gardens' is shown complete with an orchard (plates 3.1, 3.2, 3.3). Robert Miller grew apples, peaches, plums, apricots, figs, cherries and pears (Anon 1894). The orchard was surrounded by rows of pines and by *C.monogyna* hedges which acted as wind breaks (see A in fig. 3.3). Plate 3.1 is dated Circa 1890. The hedge is well established and probably of fruiting age (> 10 years old). These hedges were likely to have been established by Robert Miller from seed or plants transported from Melbourne. This then brackets the date of the 'Poplar Gardens' hedges between 1863 (when Miller settled on 'Poplar Gardens') and 1890 (approximate date of the photograph).

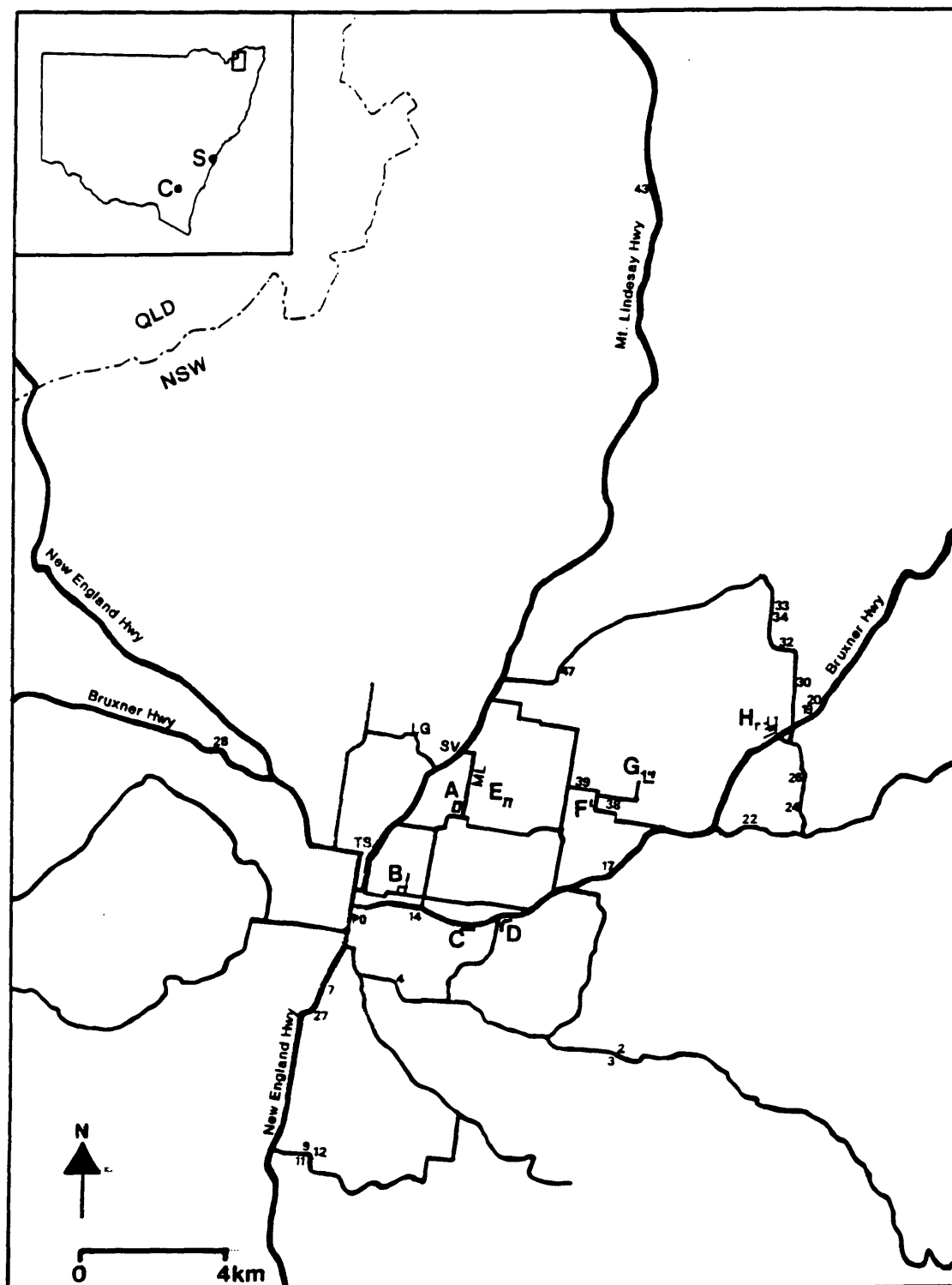


Figure 3.3 Distribution of hawthorn hedges (A-H) and trees felled for age determination indicated by numbers at Tenterfield in 1990. ML = Miller's Lane, LG = 'Leeches Gulley', SV = 'Spring Valley', TS = 'Tenterfield Station'. Qld = Queensland, NSW = New South Wales, (-.-.-) state border. Inset shows location of study area in northern New South Wales; S = Sydney, C = Canberra.

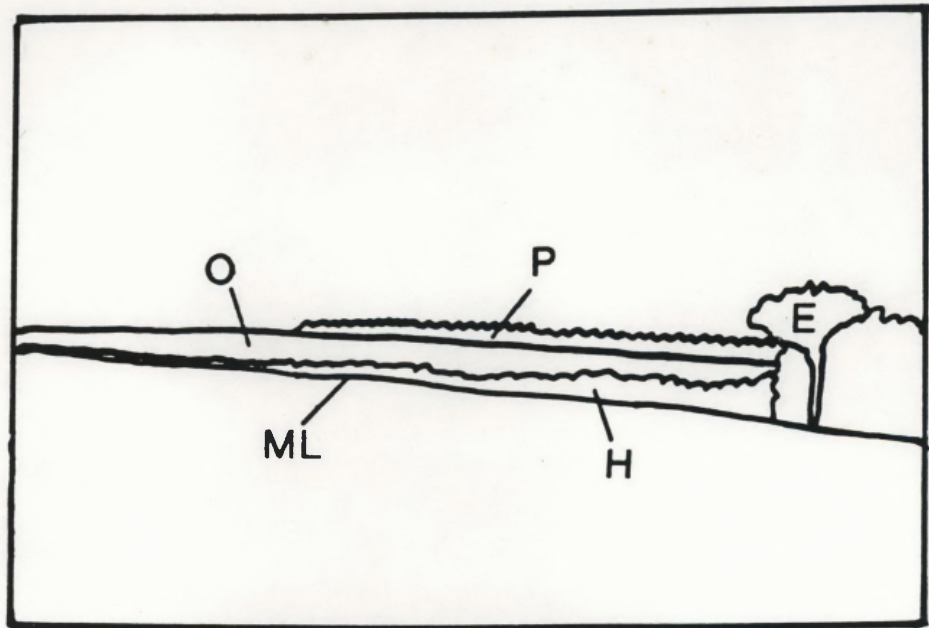
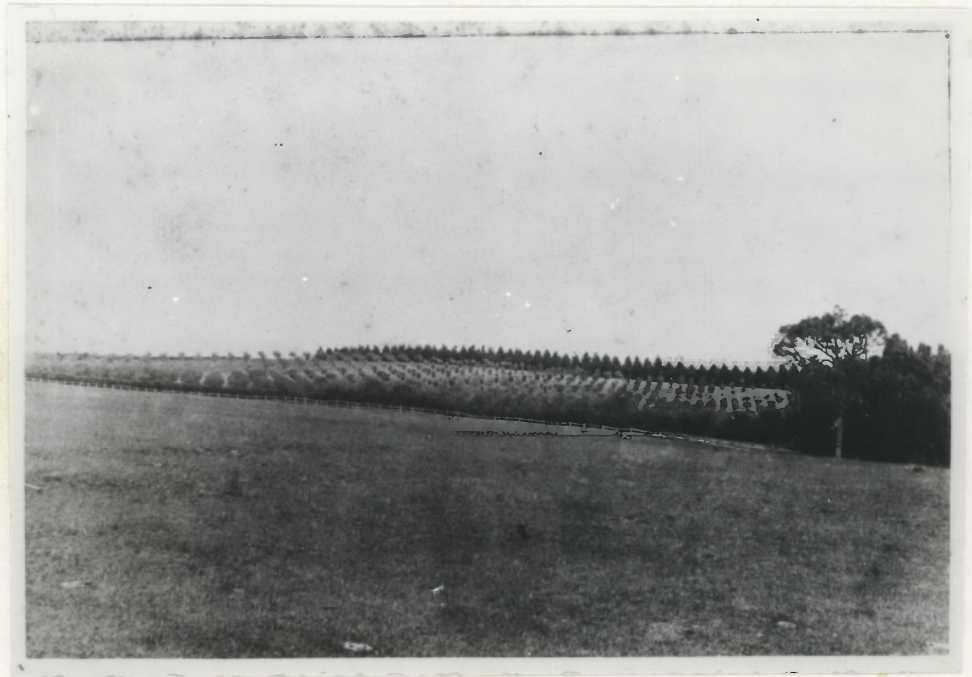


Plate 3.1 Orchard and hawthorn hedge at 'Poplar Gardens' (Circa 1890). P = pine trees, E = eucalyptus, O = orchard, H = hawthorn hedge, ML = Millar's Lane. The photograph looks west towards the pine tree hedge. Photograph by kind permission of L. Woolnough.

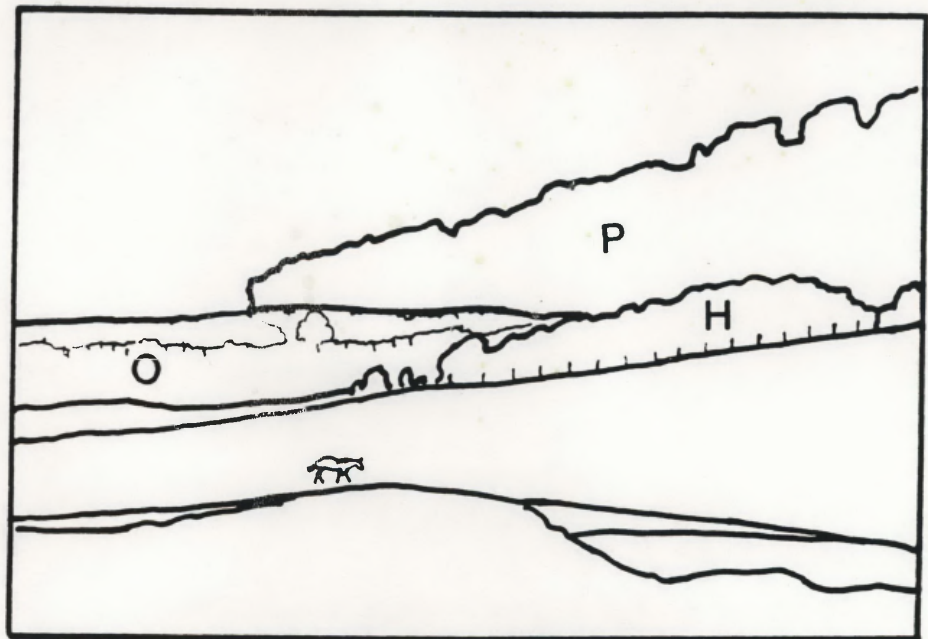


Plate 3.2 Orchard and hedge at 'Poplar Gardens' (Circa 1929). P = pine trees, O = orchard, H = hawthorn hedge. The photograph looks west towards Tenterfield. Photograph by kind permission of L. Woolnough.



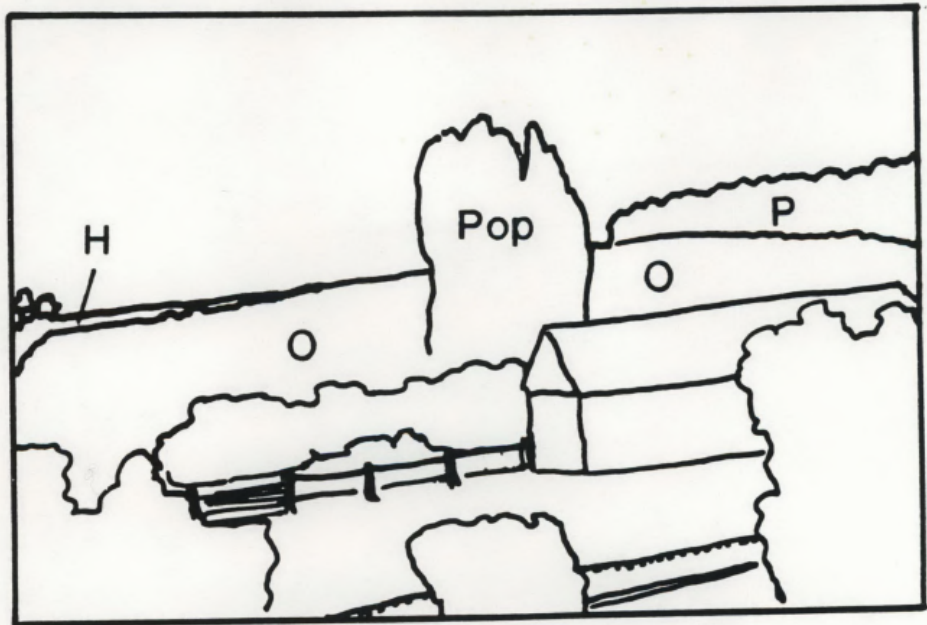


Plate 3.3 Orchard at 'Poplar Gardens' (Circa 1929). P = pine trees, O = orchard, H = hawthorn hedge, Pop = poplar trees. Photograph by kind permission of L. Woolnough.

There is still a degree of uncertainty associated with these dates. *C.monogyna* may have been introduced to the district earlier by other individuals. However in an article in the *Town and Country Journal* of 1894 later reprinted in 1936 in the *Tenterfield Star*, the local newspaper, Robert Miller was regarded as a role model and his successful enterprise induced "others to follow in his footsteps", suggesting that Miller may have been the first to extensively plant hawthorn hedges in the district. There would have been a time lag between first plantings of hawthorn and maturation to reproductive status. The age of *C.monogyna* at first fruiting depends very much on the specific characteristics of a site. Heavily shaded plants tend to fruit later. Most plants appear to fruit first between 10 and 15 years of age.

It is probable that the hedge at 'Poplar Gardens' was amongst the first in the Tenterfield district. Together Sommerlad and Miller were probably largely responsible for much of the hawthorn introduced to the Tenterfield area. The orchard at 'Poplar Gardens' has since been removed and the pines to the west have largely been removed (Plate 3.4).

Unfortunately no such detailed information exists for other hedges in the district. At least eight hedge complexes still exist in the Tenterfield district (A to H in Fig. 3.3). Some are mere remnants of their former selves or were planted just for aesthetic purpose and not as windbreaks or fencing. The hedge complex located near the intersection of Blackswamp Road and the Bruxner Highway (H in Fig. 3.3) is the largest and

most intricate of the remaining Tenterfield hedges. This hedge had a single stem aged at 55 years (felled 1990). This age probably underestimates the actual establishment of the hedge. A black and white aerial photograph (Run 14 No 80245) dated 20 October 1943 shows clearly well established hedges. Mr A. Koch a local resident on the farm where the hedges are located believed that the hedges were in existence 70 years ago (c. 1920). This is still some 50 years after the Poplar Garden hedge was probably planted. This then gives a bracket of years for the establishment of the hedges at H between 1920-1935 with a possible earliest establishment date c. 1900.

For the purposes of this study the bracket dates for the establishment of *C.monogyna* into the Tenterfield district are 1863-1890. All other plants in the district will be related back to these years and to the 'Poplar Gardens' hedge (H in Fig. 3.3) which was one of the first hedges planted in the district. This of course ignores spread from other hedges planted later. However when regarding *C.monogyna* at Tenterfield as a single large population, a net spreading rate can be obtained without reference to later establishment dates. These establishment dates for Tenterfield correspond to the general pattern of *C.monogyna* plantings elsewhere on the Northern Tablelands, c. 1890 near Ebor (see transcript in section 3.2 above and full letters in Appendix 1) and c. 1860s near Walcha (*pers comm.* Ms Alice Norton, 1989) (letters in Appendix 1).

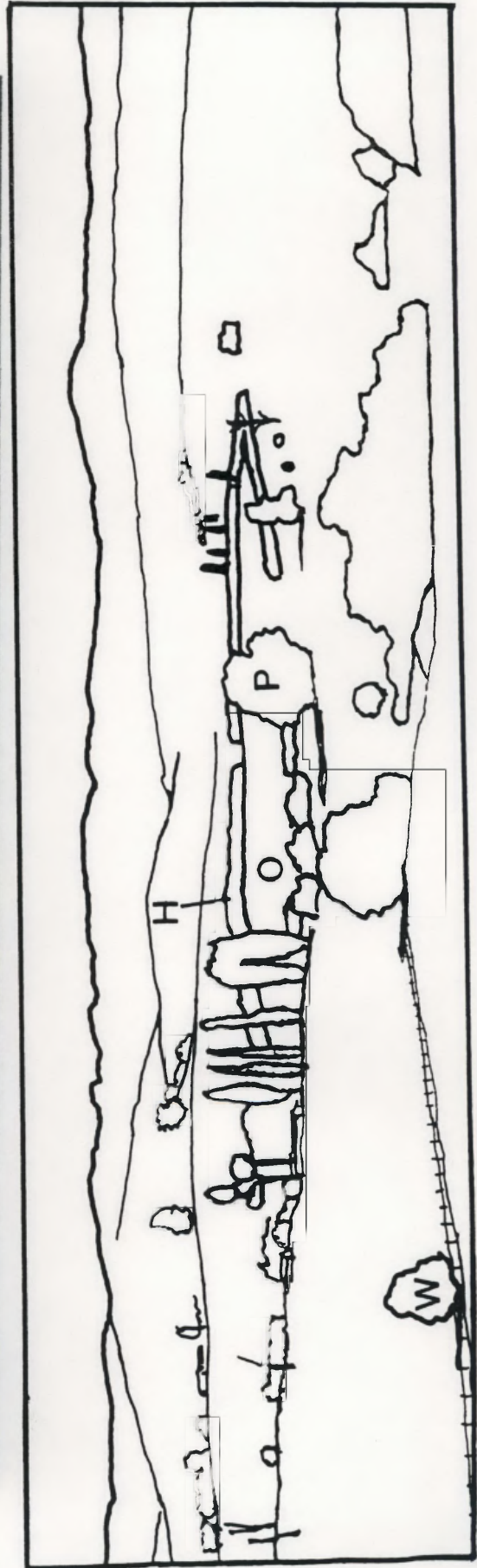
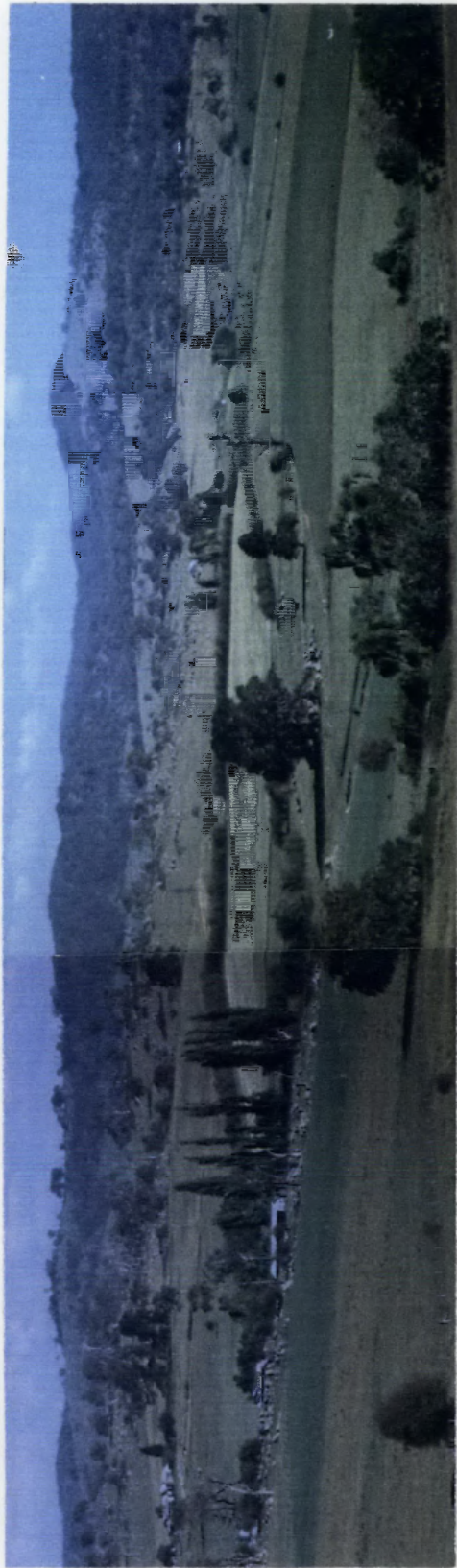


Plate 3.4 "Poplar Gardens' (Circa 1981) looking towards the south east. H = hawthorn hedge, O = site of orchard, P = old pine tree, part of previous hedge, W = wild hawthorn plant. Photograph with kind permission of L. Woolnough.

A total of 47 trees were felled and aged. Twenty three trees were excluded from the analysis as they were multiple stems of some individuals. Only the oldest were used for calculation of rates of spread. Table 3.2 shows the details of felled and aged *C.monogyna* at Tenterfield. Tree numbers refer to numbers located on Fig. 3.4 All distances and calculations of rates of spread relate to the 'Poplar Gardens' hedge (A on Fig. 3.4). Of 24 trees felled and aged the oldest were trees 7 and 27 (45 years old). These trees were located south of Tenterfield. By subtracting the age of a tree (column a) as determined by annual growth ring counts from 1990 when the trees were felled, this gave the date of establishment of the tree (column b). The difference between establishment date and the range of dates for the establishment of hedge A (column b - (1863-1890) yielded a range of times since planting of hedge A (column c). Dividing the distance of the tree to hedge A (column d) by the difference in ages of the hedge and tree (column c) gives a range of values for the rate of spread (column e). The maximum rates of spread calculated for *C.monogyna* was 152.2-198.9 m yr<sup>-1</sup> for tree 43 located 17.5 km north of Tenterfield near where the Boonoo Boonoo River crosses the Mount Lindesay Highway. This tree was approximately 500 m from the property 'Goldbrook' on which other hawthorn and *Cotoneaster* plants grew. It is likely that this tree came from seed dispersed from trees already growing on 'Goldbrook' and not directly from Tenterfield. The slowest rate of spread of 25.9 m yr<sup>-1</sup> was recorded for tree 14. The mean rate of spread using 1863 as the date of introduction of *C.monogyna* to Tenterfield is 80.2 m yr<sup>-1</sup> This estimate is lower but shows general agreement with the spread of 120 m yr<sup>-1</sup> estimated for hawthorn spreading along roadsides from Glen Innes (Smith 1982).

Table 3.2 Number, height, girth and ages of *C.monogyna* trees felled in 1990 at Tenterfield and calculated rates of spread away from the 'Poplar Gardens' hedge with an establishment date between 1863 and 1890 (A in Fig. 3.3). See text for details.

Tree No.	ht (cm)	girth (cm)	age (yr)	Column		distance (m) $y^{-1}$	rate of spread d/c
				a	b		
				est. date 1990-a	age difference a-(1863-1890)		
2	644	58	26	1964	101-74	7675	76.0-103.7
3	695	52	24	1966	103-76	7675	74.5-100.9
4	210	21	18	1972	109-82	4800	44.0-58.5
7	467	60	45	1945	82-55	5875	71.6-106.8
9	545	42	43	1947	84-57	10125	120.5-177.6
11	356	12	14	1976	113-86	10125	89.6-117.7
12	373	14	15	1975	112-85	10125	90.4-119.1
14	307	35	16	1974	111-84	2875	25.9-34.2
17	483	73	35	1955	92-65	4200	45.7-64.6
19	712	*	32	1958	95-68	10125	106.6-148.9
20	743	*	25	1965	102-75	10125	99.3-135.0
22	745	*	30	1960	97-70	7575	78.1-108.2
24	346	27	22	1968	105-78	9125	86.9-117.0
26	375	45	29	1961	98-71	9250	94.4-130.3
27	751	158	45	1945	82-55	6450	78.8-117.3
28	179	11	15	1975	112-85	6600	58.9-77.6
30	308	20.5	30	1960	97-70	9625	99.2-137.5
32	385	63	23	1967	104-77	9800	94.2-127.3
33	350	48	29	1961	98-71	10125	103.3-142.6
34	524	104	30	1960	97-70	10125	104.4-142.6
38	485	72	27	1963	100-73	4000	40.0-54.8
39	346	53	27	1963	100-73	3250	32.5-44.5
43	220	10	12	1978	115-88	17500	152.2-198.9
47	650	108	40	1950	87-60	5000	57.5-83.3

\* The base of these plants consisted of multiple fused stems, of which the oldest was used for age determination. Consequently no suitable girth measurement was made.

### 3.3 *Prunus mahaleb* in Australia

*Prunus mahaleb* was probably introduced to Australia as rootstock for commercial orchard cherries. It is possible that the *P.mahaleb* seen adjacent to the ASF (see Fig. 3.4) was either propagated as true *P.mahaleb* or it may be the result of

*P.mahaleb* rootstock being allowed to shoot and fruit on its own accord. *P.mahaleb* is still used as a rootstock for cherries as it has a number of desirable characteristics including resistance to drought and a sturdy habit (see chapter 2).

The population of *Prunus mahaleb* at ASF appears to be the only wild population of the species in New South Wales (Smith 1988) if not in the whole of Australia. The *P.mahaleb* population in ASF would not pre-date the establishment and planting of the forest as forestry practices dictated clear-felling an area before planting with *Pinus* spp. That would give the earliest date of establishment for *P.mahaleb* in the forest at about 1915.

The oldest *P.mahaleb* tree in the study plot in ASF (see Chapter 4) was a 40 year old individual felled in 1990. However a much older tree aged 70 years was felled in the same locality in 1986 (J.M.B. Smith *pers comm.* 1988). Therefore these two ages of 40 and 74 years (70 years old in 1986, add four years for equivalent age in 1990) in 1990 provide two estimates for the time of establishment of the earliest individuals in the forest, with establishment dates of 1916 and 1950. These two dates and a location in the middle of the main infestation of *P.mahaleb* in ASF (see Fig. 3.4) were used to calculate rates of spread of *P.mahaleb* (see section 3.2.1).

Figure 3.4 shows the distribution of *P.mahaleb* in and around ASF, the outlying individuals and the location of felled and

aged trees. Table 3.3 shows the size, distance to the centre of the main infestation of *P.mahaleb*, age of felled trees and the calculated rates of spread. The same procedure used for the calculation of rates of spread for *C.monogyna* at Tenterfield were used for *P.mahaleb*.

Table 3.3 Ages of *P.mahaleb* trees felled from ASF in 1990. Rates of spread are calculated from the centre of the main infestation (point x in Fig. 3.4)

Tree No.	ht (cm)	a age (yr)	b est. date 1990-a	Column	d distance (m)	e rate of spread $m\ yr^{-1}$ d/c
				c age difference a-(1916-1950) (yr)		
1	325	22	1968	52-18	1066	20.5-59.2
2	600	26	1964	48-14	978	20.4-69.9
3	600	36	1954	38-4	739	19.4-184.8
4	450	32	1958	42-8	1112	26.5-139.0
5	450	22 <sup>1</sup>	1968	52-18	1175	22.6-65.3

1 This tree had a rotted middle section. Therefore the age of 22 years is a minimum and underestimates the age of the tree and hence underestimates the calculated rate of spread.

The rates of spread range between  $19.4\ m\ yr^{-1}$  to  $184.8\ m\ yr^{-1}$ . The rates of spread calculated for an establishment date of 1950 naturally show a markedly larger variation ( $59.2\ m\ yr^{-1}$  to  $184.8\ m\ yr^{-1}$ ) compared to those calculated for an establishment date of 1916 ( $19.4\ m\ yr^{-1}$  to  $26.5\ m\ yr^{-1}$ ). Although relatively few trees were felled for analysis they were individuals at the extremity of the range rather than from individuals located well inside the population range



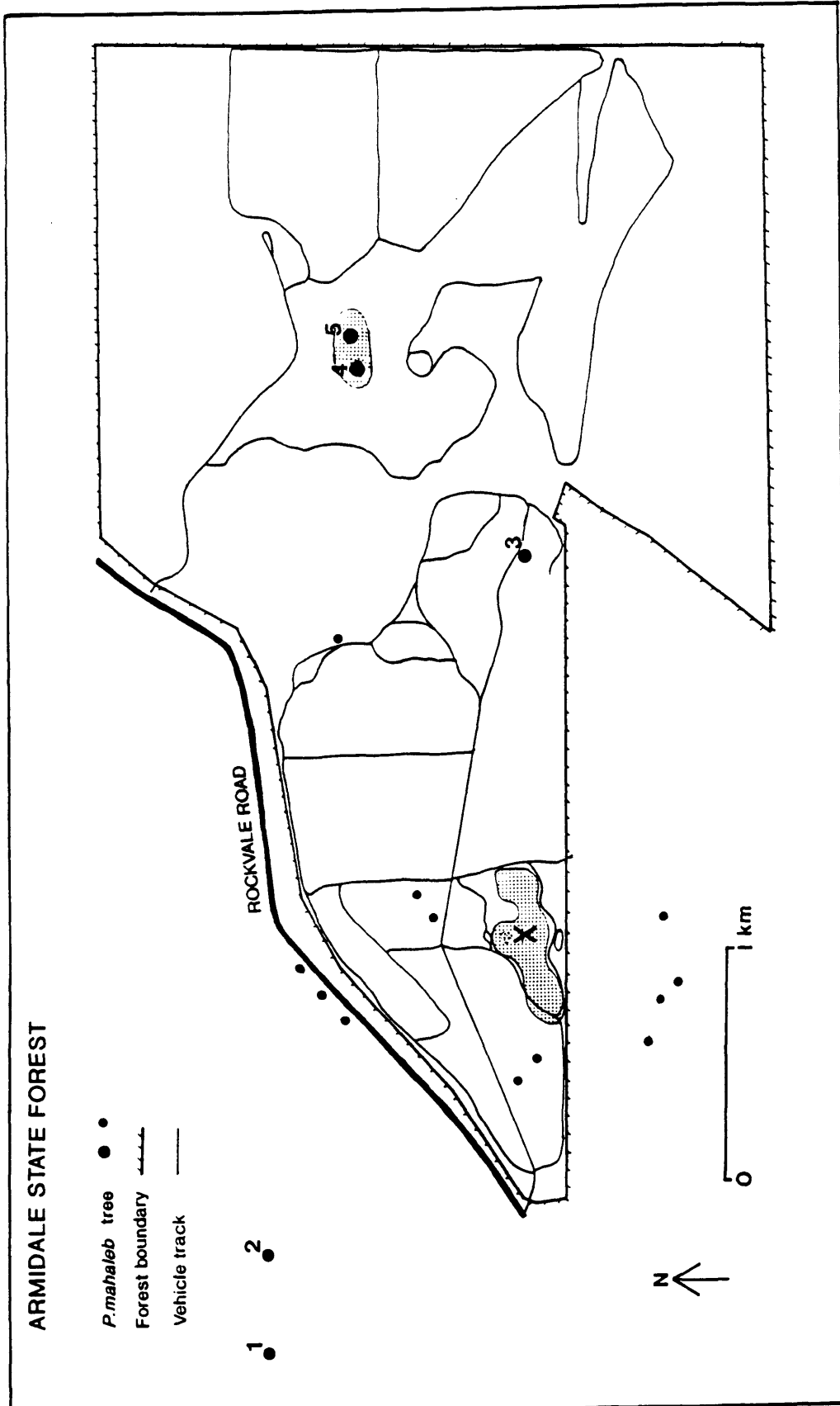


Figure 3.4 Distribution of *P. mahaleb* in around the Armidale State Forest in 1994. Stippled areas represent dense thickets. Numbers refer to felled trees (see Table 3.3). Distance in Table 3.3 taken from X.

boundaries. Consequently these rates of spread are more representative of the likely actual (maximum) rates of population spread of *P.mahaleb* at ASF.

### 3.4. Comparison of the rates of spread of *Crataegus monogyna* and *Prunus mahaleb* in Australia

The rates of spread of *C.monogyna* and *P.mahaleb* differ by a factor of about four. *C.monogyna* at Tenterfield has a mean rate of spread approaching  $80 \text{ m yr}^{-1}$  compared to *P.mahaleb* which has a mean near  $20 \text{ m yr}^{-1}$ . It is interesting to note that there is still a large range of rates of spread calculated for *C.monogyna* at Tenterfield. This could reflect two scales of seed dispersal. One, encompassing short-distance events reflect common vertebrate facilitated seed-dispersal. The second is relatively rarer long-distance dispersal events which are intrinsically more important for spread and perhaps for migration of species (Birks 1989).

These long-distance dispersal events may be attributed to dispersal by wild vertebrates (see Chapter 5) and/or to the actions of humans in the region. *C.monogyna* was a useful and familiar species suited to the climate of the region. It was an integral part of the Tenterfield landscape and propagation material was passed between neighbours and orchardists (L. Woolnough *pers comm.* 1994). It is probable that there were more hedges in Tenterfield than currently remain, as exemplified by the removal of hedges around the Sommerlad orchards north of the Poplar Gardens hedge (Ms J. Rickard *pers*

comm. 1989). The influence of humans in the spread of *C.monogyna* may have been substantial, and additional to that of wild vertebrates. The isolated *C.monogyna* plants near the Boonoo Boonoo River where it crosses the Mount Lindesay Highway (plant 43 on Fig.3.4) would in all probability have originated from plants first transported to 'Golbrook' (c. 17.5 km north of Tenterfield) and then dispersed from 'Golbrook' to the present site. The fast rate of spread ( $152.2 \text{ m yr}^{-1}$ ), although feasible by birds (see Chapter 5), might appear unlikely as there are large intervening tracts of relatively unbroken forest with little chance for establishment of seedlings, therefore necessitating a single extremely long and unlikely vertebrate-facilitated dispersal event of c. 17.5 km.

This contrasts greatly with the probably relatively much smaller human influence on spread of *P.mahaleb*. It is probable that *P.mahaleb* arrived in ASF by accident (perhaps the result of a chance dispersal event) and there it stayed unnoticed and left to its own devices. The marked differences between the two species can in part be explained by hedges acting as multiple loci of spread for *C.monogyna* with subsequent rapid areal spread, contrasted with spread from a single focus for *P.mahaleb* in ASF (*sensu* Mack 1985).

With its faster rate of spread *C.monogyna* can certainly be regarded as more invasive than *P.mahaleb* but the underlying cause of this difference in spreading rate remains unclear. Humans certainly have had an important role in the spread of

*C.monogyna* in the Tenterfield region and indeed throughout south eastern Australia by comparison with *P.mahaleb*. But it is likely that there are additional inherent biological reasons, involving population growth rates or adaptations for dispersal, that may better explain observed differences in the rates of spread of the two species. Are the two species acting in some individualistic manner that makes *C.monogyna* more invasive and *P.mahaleb* less so? To address this, Chapter 4 investigates the population dynamics and Chapter 5 compares the dispersal ecologies of both species.