CHAPTER 6. DISCUSSION AND CONCLUSIONS

6.1 Overview of biological invasions

A range of factors might be expected to contribute to successful invasion by a plant. These include climatic and edaphic similarities of source and recipient environments, rapid population growth, effective dispersal, avoidance or escape from predators, pathogens and competitors, a generalist strategy, and initial disturbance in the receiving community (see sections 1.1.6, 1.1.7). However these 'guidelines' do not hold for all invaders, nor do they ensure success (Barrett and Richardson 1986, Holdgate 1986, Mooney and Drake 1989, Groves 1986a, Roy 1990).

The concentration of research on characterizing successful invasions needs to be balanced by equivalent research of unsuccessful invasions (di Castri 1989, Groves 1986a, Holdgate 1986). This project addresses this need by providing data on differential success, or more specifically relative invasiveness, of two closely related invading plants. It accomplishes this by combining an integrated historical, demographic and ecological approach, similar in scope to Vitousek and Walker's (1989) study of the invasion by *Myrica faya* in Hawaii but with the added dimension of comparison with a less invasive species.

Invasion of Australian ecosystems by a multitude of introduced species facilitated by European settlement has led to tremendous upheaval and dislocation of ecosystem processes (Adamson and Fox 1982, Fox and Adamson 1986). The financial and ecological cost has been, and will continue to be immense. To understand the processes of biological invasions, and to recognize their impacts, are the first steps to conserving and managing ecosystems for future generations.

6.2 The specific outcomes of the project

It is useful at this stage to summarize the principle findings of this project, to highlight both the similarities and the differences between *C.monogyna* and *P.mahaleb*.

1. *C.monogyna* and *P.mahaleb* are two relatively closely related species with similar growth forms, breeding systems and overlapping home ranges in central and southern Europe (Chapter 2).

2. *C.monogyna* and *P.mahaleb* were intentionally introduced to Australia in the nineteenth and twentieth centuries and have succeeded in establishing naturalized populations in south eastern Australia (Chapters 2 and 3).

3. *C.monogyna* has attained a much wider distribution and overall larger naturalized population in Australia than *P.mahaleb* (Chapter 2) principally as a result of extensive planting of *C.monogyna* in hedges.

4. *C.monogyna* has spread at a rate between 80-120 m yr^{-1}, at least four times faster than *P.mahaleb* which is spreading at 20 m yr^{-1} (Chapter 3).

5. *C.monogyna* has a slower projected population growth than *P.mahaleb*. However most of the population growth in *P.mahaleb* is directed towards seedlings located beneath large parent plants (Chapter 4).

6. *C.monogyna* and *P.mahaleb* have very different seed dispersal ecologies as a result of different fruiting phenologies (Chapter 5). *C.monogyna*, a winter fruiting species, is preadapted for long distance dispersal by Pied Currawongs over many kilometres whereas *P.mahaleb*, a summer fruiting species, is dispersed principally by Noisy Friarbirds over much shorter distances of < 100 m.

6.3 Reasons for the differences in relative invasiveness of *Crataegus monogyna* and *Prunus mahaleb*.

Both *C.monogyna* and *P.mahaleb* are successful invaders in temperate Australia. After having arrived in Australia, both have established and spread, and are now incorporated into Australia's naturalized flora. Despite both being successful invaders they differ markedly in their invasiveness.

6.3.1 Rate of spread of *Crataegus monogyna* and *Prunus mahaleb*.

Considerable differences exist between the rate of spread of both species in Australia. *C.monogyna* has measured rates of spread four to six times greater than the spreading rate of *P.mahaleb*.

From an historical perspective *C.monogyna* has had a 'head start' in Australia compared to *P.mahaleb*. This difference comes about largely as a result of *C.monogyna* being introduced for cultural and aesthetic reasons, which meant that it was propagated and distributed widely (Chapter 3). *P.mahaleb* on the other hand was introduced primarily as a rootstock for commercial cherries. As a result *P.mahaleb* was restricted to specific locations. Under this horticultural management regime it did not 'run wild' except in a single location.

The considerable influence of humans in spreading invaders should not be understated. Intentional plantings of *C.monogyna* in hedges and in gardens and the role of these plantings as foci for further spread (Chapter 3 and Mack 1985) should be seen as a major determinant of the greater invasiveness of *C.monogyna*. *P.mahaleb* conversely was restricted to a single locality and not planted widely. Widespread planting as rootstock for some orchard fruits may represent a potential risk in the future. In the meantime orchard management suppresses the reproductive capacity of *P.mahaleb* in those localities. Orchard abandonment and subsequent 'escape' of *P.mahaleb* may become an issue in the future.

6.3.2 Population growth of *Crataegus monogyna* and *Prunus mahaleb*.

It might appear that invading species must have rapid rates of population growth compared to non-invading species. Likewise a more invasive species would be expected to have a higher rate of population growth than a less invasive but otherwise similar species. Contrary to expectations, *C.monogyna* with demonstrably faster rates of spread, had consistently slower rates of projected population growth than *P.mahaleb* (Chapter 4). However the nature of population growth is very important. Most population growth in *P.mahaleb* is concentrated in the seedling class and is largely confined to the immediate vicinity of the parent plant. Fecundity estimates based on dispersed *P.mahaleb* seedlings result in projected population growth rates for *P.mahaleb* approaching those for *C.monogyna* (Table 4.20, 4.21).

The higher rate of population growth of *P.mahaleb* is not translated into more rapid areal expansion of the population. *P.mahaleb* in ASF is dominated by a few old fecund individuals which provide a central focus for reproduction, recruitment and population growth (Fig 4.1b). *C.monogyna* has a much wider spread of ages (Fig 4.1a) and suggests recruitment from seed dispersed from plants located over a much larger geographical area.

Together, the population growth of *P.mahaleb* concentrated under parent plants and solely local source of seedling recruits, promote a lower relative invasiveness for *P.mahaleb* compared with *C.monogyna.* This last point leads this discussion to the importance of seed dispersal in both species as a factor affecting invasiveness.

6.3.3 Dispersal ecologies of *C.monogyna* and *P.mahaleb.*

Both species are dispersed by a range of birds and mammals and consequently are expanding their population ranges in Australia. *C.monogyna* is an autumn-winter fruiting species while *P.mahaleb* fruits in summer. As a result the type and behaviour of seed dispersers of both species differ.

It has been variously reported that alien vertebrates are very important in the invasion by plants as a disturbance factor or more usually a dispersal vector (e.g. Vitousek 1990, Vitousek and Walker 1989 - *Myrica faya* in Hawaii; Huenneke and Vitousek 1990 - *Psidium cattleianum* in Hawaii; Fox 1990 - alien plants in urban areas). The majority of seed dispersal in *C.monogyna* and *P.mahaleb* at Armidale is by native birds - Pied Currawongs and Noisy Friarbirds, with a negligible role for any introduced birds. Likewise native mammals also disperse seeds of these species, although the relative importance of these animals is less clear.

Pied Currawongs are the main dispersal agent of *C.monogyna* in Armidale. These birds congregate in large numbers in Armidale during autumn and winter (Fig. 5.1). The behaviour of Pied Currawongs at this time is conducive to extensive long-distance dispersal over many kilometres. This long-distance dispersal is augmented by short-distance seed dispersal by other birds and ground and arboreal mammals.

This pattern contrasts significantly with the summer fruiting *P.mahaleb* which has its seeds dispersed by birds and mammals over distances generally less than 70 m (Fig. 5.9), with only rare long-distance events.

Prunus mahaleb does however (perhaps surprisingly for an alien plant) display a relatively efficient dispersal system by comparison with the situation in its native range. Herrera and Jordano (1981) provided detailed information on the avian dispersal system of *P.mahaleb* including some anecdotal information on mammals. Reference to dispersal of *P.mahaleb* seeds, particularly in relation to fruit traits, appears in Herrera (1987, 1989), Debussche and Isenmann (1989) and Guitan *et al.* (1992). In these studies it was shown that a variety of birds and ground-dwelling mammals dispersed *P.mahaleb* seeds, though all dispersal agents differed in quality and quantity of dispersal. Herrera and Jordano (1981) showed that most seed dispersal occurred over distances < 50 m which is comparable to dispersal distances achieved in Australia.

Prunus mahaleb is characterized by intense fruiting. The production of a very large fruit crop over a very short time and in a restricted location encourages fidelity in potential dispersers. Animals do not have to travel far nor spend long times searching for fruit. The fruit is on the whole nutritionally poor but with a high sugar content. This may provide a readily digestible source of food to sustain animals while they search out other foods. The dense growth of *P.mahaleb* and the pine overstorey in ASF provides protection for dispersers from predators. This system promotes effective short distance (< 70 m) dispersal.

Another factor which also promotes short distance dispersal is that *P.mahaleb* fruit does not remain indefinitely in the canopy. All fruit whether dispersed by animals or not has disappeared by February. A large proportion falls beneath the canopy. This is a major factor promoting high seedling densities under parent trees (see Chapter 4).

The inherent variability of dispersal of *P.mahaleb* in its home range (Guitian *et al.*1992) is likely to promote a generalist dispersal strategy which facilitates access to a wide variety of dispersal vectors (Sallabanks and Courtney 1993) and hence long term success even in new habitats. The wide range of dispersers of *P.mahaleb* in Australia provides a variety of dispersal quality likely to facilitate continued localized range expansion of *P.mahaleb* near Armidale. In this regard *P.mahaleb* can be seen as a successful invader, albeit less so than *C.monogyna*.

Similarly *C.monogyna* in Europe is adapted to fruiting in autumn and winter coincident with the presence of migrant birds in large numbers which disperse *C.monogyna* seeds (Debussche and Isenmann 1990). Therefore *C.monogyna* is preadapted to exploit altitudinal and latitudinal migrant birds in Australia e.g. Silvereyes, Noisy Friarbirds and Pied Currawongs, a factor which would ensure successful invasion and at a faster rate of spread of *C.monogyna* in Australia.

A key to recognizing potential invasiveness of plants is to assess their dispersal systems in their home ranges and then translate these characteristics to Australian ecosystems. This takes a functional approach to characterizing invasions. This is particularly important where humans have promoted significant structural and functional changes in recipient communities.

6.4 The relative importance of humans, plant demography and seed dispersal in determining invasiveness of *Crataegus monogyna* and *Prunus mahaleb*.

The significance of humans and seed dispersal in the course of the invasions of *C.monogyna* and *P.mahaleb* together determine the different invasiveness of each species. While humans and natural seed dispersal are both important factors in the establishment of alien plants (Heatwole and Walker 1989) it is difficult to ascertain which is more important.

C.monogyna has had a significant 'head start' over *P.mahaleb* by widespread introduction and planting as hedge and ornamental plants. This has resulted in numerous introduction foci, which all else being equal, will result in a faster rate of range expansion (Mack 1985) and hence invasiveness. Newsome and Noble (1986) suggested that humans are relatively more important in determining the nature of invasions than long distance seed dispersal. However realization of invasiveness must depend upon suitable seed dispersal (Holdgate 1986, Bazzaz 1986, Noble 1989). Not all introduced plants will be assured of fast rates of spread and high rates of establishment and naturalization.

Current levels of naturalized 'wild' *Cotoneaster* plants in Armidale (Fig. 5.7) suggest that the effort of planting by humans (Fig. 5.6) does not ensure proportional representation among established wild plants. Mulvaney (1986) examined the relationship between government nursery sales of *Cotoneaster* and *Pyracantha* and the number of wild plants established in bushland around Canberra. Despite much higher sales, *Cotoneaster* has far fewer wild individuals growing in bushland. A similar suite of avian dispersers available to ornamental plants in Canberra is also available in Armidale. The key factor in Armidale (and probably in Canberra) is that *Cotoneaster* has not been incorporated into the diet of the major seed disperser, Pied Currawongs. There must be some seed dispersal of *Cotoneaster;* rarely by Pied Currawongs, but probably by Silvereyes and Starlings. Brush-tailed possums and macropods also may disperse *Cotoneaster* as faeces of these animals occasionally contained *Cotoneaster* seeds (D.Bass *pers observation* 1988-1991). However this dispersal is eclipsed by the current massive dispersal of *Pyracantha* and *Ligustrum* by Pied Currawongs, which are both well represented by many wild individuals.

The invasion by fleshy fruiting woody plants in the Armidale region described in the present study exemplifies the value of Roy's (1990) mixed approach that investigates the relationships between invader and environment. It is intrinsically more useful as it recognizes the multiplicity of factors and interactions that ultimately determine the nature and direction of biological invasions. Provided the receiving environment is suitable for colonization by an invader, plant-animal interactions, in particular seed dispersal, is critical in the spread of invading plants (Holdgate 1986, Johnstone 1986).

Invading fleshy fruiting plants will in general be characterized by positive and rapid population growth, will often have been widely planted by humans, and will have effective dispersal of seeds away from parent plants. More effective seed dispersal (in terms of number of seeds, distance of dispersal, and arrival in safe sites) will facilitate higher rates of spread.

6.5 Management of invasions by fleshy fruiting woody plants.

6.5.1 Impact of fleshy fruiting woody plants.

This study reveals widespread ingestion by vertebrates of fruit of alien woody plants in Armidale. It is likely that there is a range of direct and indirect consequences for plant and animal communities invaded by these plants. The most striking effect of invasion by fleshy fruiting woody plants in Armidale concerns Pied Currawongs. Elsewhere, Pied Currawongs have been implicated in increased predation on smaller native birds. It is likely that a similar situation also exists in Armidale. Dr H. Recher (*pers comm.* 1990) suggested that high rates (of up to 100%) of nestling predation near Mt Duval, north of Armidale can be attributed to Pied Currawongs. This may be an indirect consequence of higher over-winter survival of Pied Currawongs facilitated by feeding on large amounts of introduced fruit in winter when other native food sources are less abundant (Recher and Lim 1990).

Not all impacts of invading fleshy fruiting plants are likely to be negative. In communities where there has been significant vegetation clearance, the invasion by fruiting shrub and tree species may yield significant temporary benefits (Loyn and French 1991) e.g. camphor laurel (*Cinnamomum camphora*) provides winter food and 'stepping stones' between rainforest fragments for native frugivorous pigeons in north eastern New South Wales (Date *et al.* 1991). *C.monogyna* has invaded agricultural grazing land which was substantially cleared in order to promote growth of pasture for cattle and sheep grazing (Curtis 1989). This has led to a reduction in habitat for some vertebrates, especially birds (Recher 1986, Ford and Bell 1981). The remaining trees on the Northern Tablelands suffer from periodic defoliation by insects which has caused a further decline in tree abundance through dieback (Heatwole and Lowman 1986). *C.monogyna* which has invaded into these areas provide food, feeding substrates, shelter and nesting sites for birds (D.Bass *pers. observations* 1988-1991).

C.monogyna also provides valuable shelter for stock from the cold south to westerly winds (Mr R. Vyner of 'Newby Park' *pers. comm.* 1988)

The entire range of ecosystem impacts by invading fleshy fruiting plants is largely unknown, very speculative, and requires significant research. Many impacts may not have had a chance to trickle through ecosystems and may only become obvious in the future.

Any control measures instigated against either *C.monogyna*, *P.mahaleb*, or any other introduced species must be made in the light of the role these introduced species play in modified ecosystems and the long term strategies of environmental managers.

6.5.2 'Weak points' in the life histories of *Crataegus monogyna* and *Prunus mahaleb*.

An important use of Leslie matrices is that elements of each transition matrix can be manipulated to simulate changes to survival and fecundity. The models can be run with these changes to see what effect they may have on projected population growth rates (Caswell 1989).

These manipulations may identify possible 'weak points' in the life cycles of pests, including invading plants. The purpose of these exercises would be to direct control strategies at particular stages in the life cycles of organisms. Forestry and Fisheries researchers have also made use of matrix models to simulate harvest strategies upon commercial resources (Begon and Mortimer 1986, Begon *et al.* 1990).

Tables 6.1, 6.2, 6.3, 6.4 show the changes in the projected population growth with a 50% reduction in the survival of individuals in each size class of the transition matrices developed in Chapter 4. Projected population growth was also calculated for a 50% and 99% reduction in fecundity.

Sensitivity analysis (Caswell 1989, Enright and Watson 1991), which compares influence on the latent root of transition matrices with changes in the individual elements of the matrices, can identify sensitive stages in the life cycle of an organism. Using a 50% reduction in survival in each class, log sensitivity was plotted for each stage (size class) of the four population matrices constructed in Chapter 4 (Fig. 6.1 a,b,c,d). In each case the proportion of individuals moving into successive classes (G_i in matrix, Table 4.4) and those that remained in the same class (P_i in matrix, Table 4.4) changed by the amounts shown in Tables 6.1-6.4. In all cases the most sensitive component was the proportion of seedlings moving into the next size class (G_i). This trend is similar to that reported by Enright and Watson (1991), where seedling and prereproductive classes were the most sensitive. Sensitivities declined in the larger size classes for both species.

The proportionately larger reduction of population growth rate attained by reducing survival in the seedling class (higher sensitivity) suggests that this the most vulnerable stage in the life cycle of both species. Significant in all manipulations is that a large reduction in fecundity has a relatively small effect on projected population growth.

By far the largest reduction in projected population growth was attained by reducing survival across the entire population. These manipulations only dealt with survival. A reduction in growth rates would have the effect of slowing transitions between size classes and thereby slowing population growth.

Table 6.1 Simulated effects of changing survival rates at various stages of *C.monogyna* at ASF. Size classes are based on height.

Size class at which reduction was applied	% reduction in survival	Value changed in matrix From-to	Calculated latent root from altered matrix
Unmodified data	None	No changes	1.13804
height (cm)			
0-100	50%	0.9055-0.4528 0.0269-0.0134	1.04541
100.1-200	50%	0.8463-0.4232 0.1385-0.0692	1.05548
200.1-300	50%	0.8695-0.4348 0.1074-0.0537	1.05929
300.1-400	50%	0.6552-0.3276 0.3448-0.1724	1.10612
400.1-500	50%	0.5179-0.2590 0.4821-0.2411	1.11765
>500	50%	1.0000-0.5000	1.11412
Fecundity	50%	all fecundity values	1.09764
Fecundity[1]	99%	all fecundity values	1.05431
All size classes	50%		0.59345
All size classes > 100 cm tall	50%		0.92387

1 All values were set to 0 except the >500 class which was set to 1.

Table 6.2 Simulated effects of changing survival rates at various stages of *C.monogyna* at ASF. Size classes are based on height for plants 0-100 cm tall and basal circumferences for plants > 100 cm tall.

Size class at which reduction was applied	% reduction in survival	Value changed in matrix From-to	Calculated latent root from altered matrix
Unmodified data	None	No changes	1.10293
height (cm)			
0-100	50%	0.9055-0.4528 0.0269-0.0134	1.03647
basal circumference (cm)			
0-5	50%	0.8666-0.4333 0.1006-0.0503	1.04243
5.1-10	50%	0.8444-0.4222 0.1515-0.0754	1.04500
10.1-15	50%	0.7493-0.3747 0.2373-0.1186	1.05521
15.1-20	50%	0.7143-0.3572 0.2857-0.1429	1.06319
20.1-25	50%	0.5769-0.2885 0.4231-0.2116	1.07540
25.1-30	50%	0.6146-0.3073 0.3755-0.1878	1.07927
30.1-35	50%	0.7143-0.3572 0.2857-0.1429	1.08349
>35	50%	0.9895-0.4948	1.08877
Fecundity	50%	all fecundity values	1.07053
Fecundity[1]	99%	all fecundity values	1.04121
All classes	50%		0.5659
All classes > 100 cm tall	50%		1.90696

1 Fecundity values were less than 1 for most elements. For the purposes of this example all values were set to 0 except for classes 30.1-35 and >35 which were set to 1.

Table 6.3 Simulated effects of changing survival rates at various stages of *P.mahaleb* at ASF. Size classes are based on height. Numbers in brackets refer to seedling survival rates away from nursery trees.

Size class at which reduction was applied	% reduction in survival	Value changed in matrix From-to	Calculated latent root from altered matrix
Unmodified data	None	No changes	1.71346 (1.22431)
height (cm)			
0-100	50%	0.8882-0.4442 0.0463-0.0231	1.47905 (1.12956)
100.1-200	50%	0.8582-0.4292 0.1233-0.0616	1.51035 (1.13437)
200.1-300	50%	0.8478-0.4239 0.1522-0.0761	1.56819 (1.13589)
300.1-400	50%	0.8889-0.4445 0.1111-0.0556	1.63469 (1.13816)
400.1-500	50%	0.4000-0.2000 0.6000-0.3000	1.69084 (1.18956)
>500	50%	1.0000-0.5000	1.69864 (1.17997)
Fecundity	50%	all fecundity values	1.56933 (1.17925)
Fecundity	99%	all fecundity values	1.16303 (1.06387)
All classes	50%		0.95041 (0.63703)
All classes > 100 cm tall	50%		1.27457 (0.90408)

Table 6.4 Simulated effects of changing survival rates at various stages of *P.mahaleb* at ASF. Size classes are based on height for plants 0-100 cm tall and basal circumferences for plants > 100 cm tall. Numbers in brackets refer to seedling survival rates under nursery trees.

Size class at which reduction was applied	% reduction in survival	Value changed in matrix From-to	Calculated latent root from altered matrix
Unmodified data	None	No changes	1.49409 (1.18559)
height (cm)			
0-100	50%	0.8882-0.4442 0.0463-0.0231	1.34379 (1.11056)
basal circumference (cm)			
0-5	50%	0.8612-0.4306 0.1130-0.0565	1.34819 (1.11434)
5.1-10	50%	0.7615-0.3808 0.2176-0.1088	1.37274 (1.12456)
10.1-15	50%	0.6154-0.3077 0.3461-0.1731	1.42045 (1.13547)
15.1-20	50%	0.6923-0.3462 0.3077-0.1539	1.44238 (1.13328)
20.1-25	50%	0.6364-0.3182 0.3636-0.1818	1.45679 (1.13874)
25.1-30	50%	0.4286-0.2143 0.5714-0.2857	1.47173 (1.15127)
30.1-35	50%	0.6250-0.3125 0.3750-0.1875	1.47646 (1.14982)
>35	50%	1.0000-0.5000	1.48231 (1.14602)
Fecundity	50%	all fecundity values	1.41080 (1.15068)
Fecundity	99%	all fecundity values	1.13775 (1.05516)
All size classes	50%		0.79859 (0.61091)
All size classes > 100 cm tall	50%		1.04236 (0.89241)

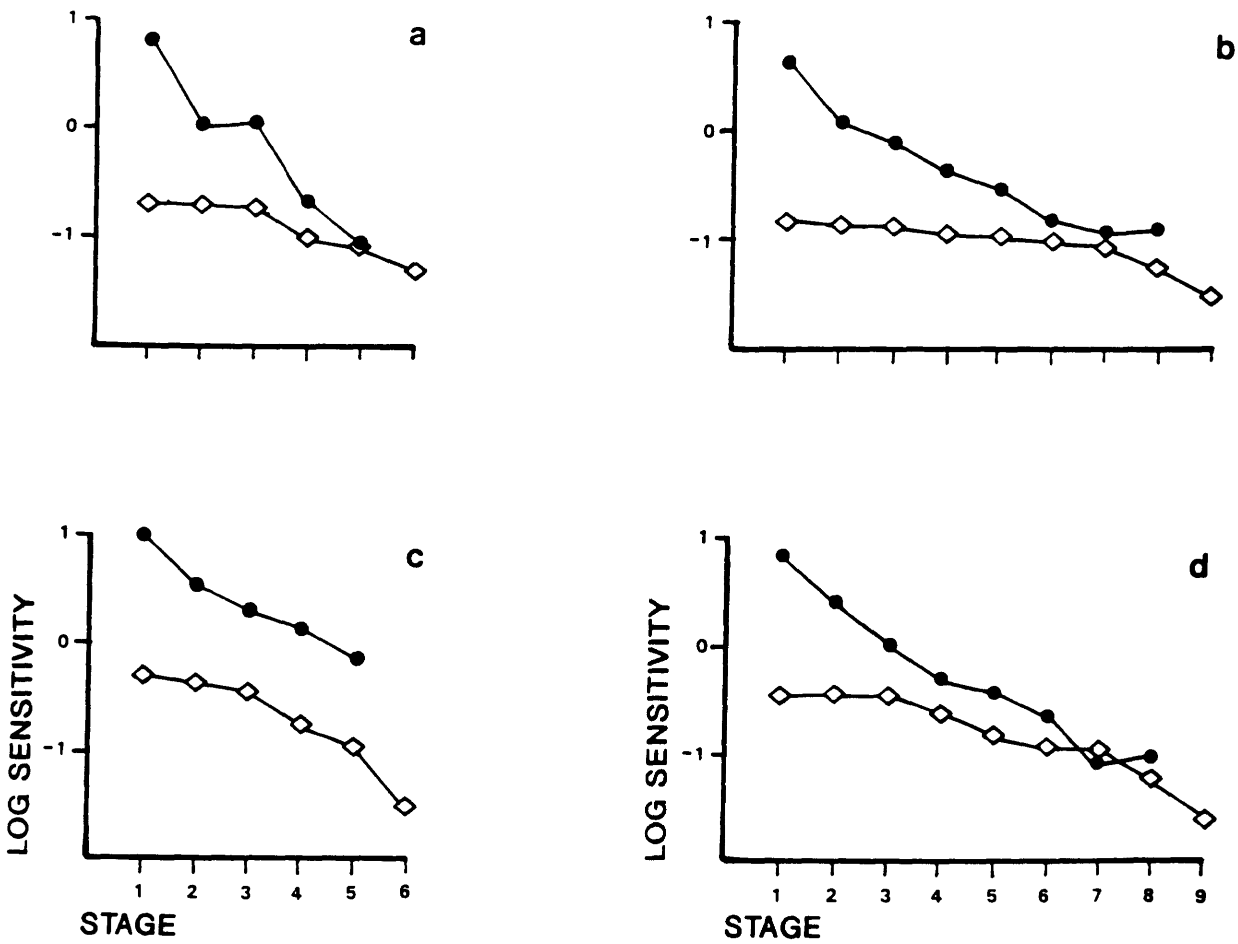

Figure 6.1 Sensitivity analysis of changes to the survival of individuals in each size class (stage). (a) and (b) sensitivity plots for *C.monogyna* height and basal circumference classified models respectively. (c) and (d) sensitivity plots for *P.mahaleb* height and basal circumference classified models respectively. Solid dots survival of individuals moving into the next size class (G_i). Open diamonds represent survival of individuals remaining in the same size class (P_i).

The importance of population growth as a factor in determining invasiveness of a species is perhaps overstated in some studies. Of much more importance here is the coupling of population growth with effective dispersal. One measure likely to reduce rates of spread of ornamental plants is the reduction of seed disperser abundance. This is both difficult and contentious. However reduction in the population of Pied Currawongs may have the added benefit of reducing predation pressure on small birds (H.Recher *pers. comm.* 1990).

6.5.3 Integrated approach to management of invasion by fleshy fruiting woody plants

The findings of this project suggest strongly that if an invading species has successfully established and is in the process of naturalization then the invasiveness of that species will depend upon the efficacy of dispersal of propagules. This process of dispersal may be facilitated by humans and 'natural' means.

The interplay of a multiplicity of abiotic and biotic factors have profound impacts on seed dispersal systems and therefore assessment of the invasive potential of a species must be made on a site by site or region by region basis. A plant regarded as a minor invasion threat in one locality may be a major problem in another because of different assemblages of plants and dispersers.

The control of an invading species is on the whole a difficult and generally expensive problem. If a species has many points of introduction and hence many invasion foci control efforts should be concentrated first on small satellite populations at the expense of larger foci (Mack 1985). The rationale for this relates to the dispersal of propagules. Small foci will have a larger proportion of propagules located near the boundary of a population and therefore well suited to explore new environments compared to large foci which have a majority of propagules located within parental patches and hence exploiting already invaded territories.

From simulations of population parameters, reductions in fecundity have little effect on population growth rates. This appears common to many long-lived perennial species (Burns and Ogden 1985, Enright and Ogden 1979). Reduction of survival in seedling classes appears to have a major influence on population growth rates. However in both situations a 50% reduction in survival of seedlings in both species still results in positive population growth. Reduction of survival in all classes results in population growth rates less than 1. Population growth rate can also be slowed in both species by reduction in growth rates which reduce the transition between class sizes. This could be accomplished by biological control; a generally very expensive alternative. The efficiency of any strategy must be assessed in terms of financial and ecological costs.

In light of the findings of this study, an integrated approach to management of invading fleshy fruiting woody plants must address the roles of humans and vertebrates in the dispersal of plants and seeds. Management of invasions should not only be reactive but should also address the causes of invasions. The widespread planting of fleshy fruiting woody plants, many of which are ornamental species compromises the integrity of natural ecosystems (Low 1988). The majority of fruiting ornamental plants were planted to attract birds into residential gardens (Pizzey 1988). Alternative native plants are available to fill this role. Planting of street trees by local councils are often dominated by introduced plants, some of which bear fleshy fruits and have their seeds dispersed by birds. *Pistacia chinensis* is such a species which is likely to increase in abundance in and near Armidale.

Changing community perceptions concerning direct and indirect effects of vegetation removal, modification, and substitution should also promote planting of local native species over introduced species (low 1988).

6.6 Recommendations for further research

This project recognizes the major role of seed dispersal in the realized range expansion of an invading ornamental plant. To understand the processes of invasion, examination of dispersal systems is crucial. In particular the role of all vertebrate dispersal agents is necessary. This study of two bird dispersed species also revealed seed dispersal by a range of native and introduced mammals that may have significant implications for other invading plants. Significantly the role of native mammals in the dispersal of native plant species is largely unexplored. Vegetation and habitat conservation and reconstruction must look at the totality of plant and animal interactions.

The investigation of impacts of invaders on ecosystems is also necessary. Cascade effects through ecosystems are important. If Pied Currawongs can maintain higher populations through winter because of the availability of introduced fruit, and then consequently exert increased predation pressure on smaller native bird species, then local and regional extinctions of avifauna may be inevitable. A large proportion of research into biodiversity decline has centred on individual agents of change. Feral cats, foxes, rabbits have all been blamed for decline in vertebrate abundance in Australia. This approach simplifies and ignores the totality of interactions between humans and the natural environment. There may be a range of similarly disastrous impacts that are not yet widely recognized which should be investigated.

6.7 Conclusion

The most important factors determining the relative invasiveness of *C.monogyna* and *P.mahaleb*, two alien fleshy fruiting woody plants in the Armidale region, are the extent and nature of planting of each species by humans and the effectiveness of their seed dispersal over long distances.

Seed dispersal is the key factor identified in this study. Even with rapid population growth, without effective seed dispersal an invading plant will not spread rapidly.

The set of generalizations concerning the potential of a plant to become invasive, such as wide climate tolerance and rapid growth (see sections 1.1.6 and 1.1.7) are still useful. However, to recognize and anticipate highly invasive fleshy fruiting species in the future, an assessment of the interactions between an introduced plant and biotic components of the receiving ecosystem is required. In particular, attention should be given to the nature of the dispersal system which will determine potential propagule dispersal and consequently rate of spread.

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APPENDIX 1

This Appendix lists the persons who provided personnel communications concerning aspects of this project. The information concerning the history of hawthorn on the northern Tablelands came in response to a media release and letters to country newspapers. The persons are listed alphabetically. Correspondence from Ms Chant, Ms Norton, Ms Rickard, Mr Woolnough has been reproduced here. Some parts of the letters have been annotated by me.

Ms Ruth Chant a local historian in Armidale provided an enlightening transcript of a conversation that she had with an elderly Armidale resident. The transcript has been partly reproduced in Chapter 3.

John Humphreys (Chapter 5) is a Senior lecturer in the Department of Geography and Planning, University of New England. His home was the location of the bird bath used in the assessment of Pied Currawong diets. John Humphreys is a keen amateur ornithologist and has kept regular records of birds at his home and on the campus of the University of New England

John Jenkins (Chapter 5) is a PhD student within the Department of Geography and Planning, University of New

England. He kept a regular eye on a breeding pair of Blackbirds in his garden in Armidale during 1989-1991.

Mr Robert Miller is an elderly resident of Armidale whose family came from Tenterfield. He is the Cousin of Lloyd Woolnough and together provided details of their family lives in Tenterfield and on the Northern Tablelands.

Ms Alice Norton is a resident of Walcha who provided information about approximate times of planting of hawthorn hedges near Walcha.

Associate Professor Harry Recher, Department of Ecosystem Management, University of New England, is a highly regarded ecologist and ornithologist. While attending a working group of bird related researches at the Newholme Field Station in the shadows of Mt Duval A/Prof. Recher revealed very high nestling predation by Pied Currawongs. He was concerned that this may go unchecked. His thoughts on culling Pied Currawongs prompted a significant public debate through the letters column in the *Sydney Morning Herald*.

Ms J. Rickard of Liston in northern New South Wales provided details about hawthorn in the Tenterfield area.

Associate Professor J.M.B. Smith, Department of Geography and Planning, University of New England provided significant information concerning some early investigations of introduced species in the Armidale region. Some of this information came in the form unpublished data, which I was able to make reference to in Chapter 5.

Mr R. Vyner who owned the property 'Newby Park', on which my Saleyards site was located provided some details concerning the grazing history of the site and the impact of hawthorn on the property.

Mr Lloyd Woolnough a former resident of Tenterfield and now residing in Gladesville in Sydney, provided a tremendous amount of historical information concerning the early settlement of Tenterfield. His own family history research uncovered useful information about Robert Miller of 'Poplar Gardens', the focus of the analysis of spread of hawthorn in Tenterfield covered in Chapter 3. He kindly provided permission to reproduce photographs of 'Poplar Gardens' which provided approximated ages for hawthorn establishment in Tenterfield.

THMD, ICAE
CH 6377 Seelisberg
Switzerland
2 - 4 - 89.

Dear David,

Thank you for your letter of 28/2. It prompted me to make some further enquiries among old Ebor residents. While I was at home I was taping some family history and I included an interview with an old neighbour - Rube McIntyre. I have transcribed the section relevant to hawthorn hedges on the back of this letter. Her visual memory for events of her youth has always been remarkable, but now she can no longer even remember how long she has been in Autumn Lodge.

Another neighbour, Mrs Jean Turnbull, who used to live at Kotupna, but now lives at Ebor told me they had a hedge there along the verandah below the kitchen, which was transplanted from a bush that had been growing there. It was unusual in that it had tomato red flowers most are white. It has now been removed.

She also quoted from a book 'Pioneering New England' by a former resident; about an 'enterprising settler' who got "sombre black stones' for his garden at Glen Innes. "A hawthorn tree flourished and is still there". His elms had come from Stonehenge. It was Ogilvies, and described what happened before 1938. She is over 80 (don't ask her age). Her brother, Bruce Winn, 92, is in Strathlea, and may be able to give you some more informatio[n]. He is probably the oldest living ex-resident.

I noticed that there are still one or two hawthorn bushes by the pine trees at 'Bonnie Brook' - covered in a long grey lichen beard. The soil is rich + thin basalt - and rainfall heavy ~ 50" p.a.

Most of the people in the district were of English ancestry. I presume the original seeds came from England, but most properties acquired seedlings from their neighbours - as a reminder of 'the old country' and its countryside. When I visited England 10 years ago - the land of my ancestors - I was amazed to find the origin for what had seemed strange customs in Australia. There the hawthorn hedges were used as windbreaks for treeless fields (near Wolverhampton). The trees were carefully pruned and woven together ("plashing" (sp?)). I had never heard of this before, though I knew they had to form a hedge by the fence and they should periodically be 'trimmed back'. Some English hedges contained other species such as elder trees. The one at 'Bonnie Brook' included some honeysuckle and a dog rose. The chooks sometimes went off and made their nests under it.

Another quaint custom my father inherited from his father: take the stone off the potato paddock and stack it into low walls by the fence. It made excellent harbour for snakes. In England I saw the same pattern of making stone walls in treeless areas - to reduce the wind on the sheep. But they were using flat sedimentary rocks, and it doesn't look so tidy when you try the same thing with basalt. My grandfather's grandfather and his brother originally came from the Somerset area. Same hay-making principles were applied, but Ebor's wet summers are not very conducive.

I hope all this rave may be of some interest,

Yours sincerely

Ruth Grant.

Transcript from a tape of a conversation with Rube McIntyre, ~93, formerly of Milamba, Guy Fawkes – made on 14/3/1987

RC. Do you remember the hawthorn hedge? [refers to 'Bonnie Brook']

RM. By Jove, do I!

RC. When was that planted, that hawthorn hedge?

RM Oh, in Taylors 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 ~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 heh heh! I don't like thorny things like that.

RC: Where did your dad get them from?

RM: Taylors – 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.

SC: 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 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.

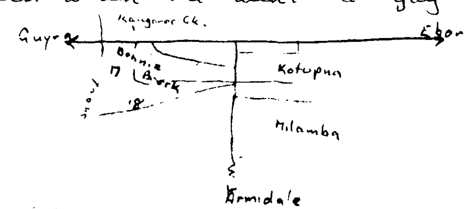
RC: He got rid of them at Kotupna too, did he?

RM. Yeah, yeah.

RC: When did you dad go up there?

RM: Oh, dad wasn't married when he went to Guy Fawkes firs

map of properties mentioned



History

RM. 'Old Mr Turnbull selected Guy Fawkes' (Kotupna) 'Tom Turnbull a real good-living ma

'Milamba' – selected by McIntyre – Rube's father.

'Bonnie Brook' – seems to have been selected by Tom Taylor. He came by home (BB) .. and remembered the hedge. In 1908 he sold lot 17 to Robert Chant, my grandfather. Rube M remembers the day he took his Milking Durhams (cows) up from Alstonville, as they went by the school (on Milamba). The teacher (PJ Flinn) told them to stop looking. Probably at the same time he sold lot 18 to John Hackett, who in 1922 resold it to Robert Chant.

Tiara
Walcha
10/12/89.

JB/MW

Dear Mr Barr,

You have certainly chosen a difficult study!! I don't think that too many - if any - people kept very early gardening - or beautification records, very early in New England -

We have Hawthorns here on our property - It was first taken up in 1840 by 2 brothers, the McNabs, and I am sure that they planted nothing here - My grandfather came here in 1853, & both grandparents, grandmother in particular loved trees & gardens, & planted a long hawthorn hedge. This hedge is still here, & now trimmed & looks very well. Unfortunately, birds carry the seeds, and this year my nephew dozed out some of the large bushes which were dotted about the house paddock, & poisoned some - I don't know what he used to do this -

In all our other paddocks there are no problems of this kind. The sheep seem to eat any small plants -

As to the time-span - I think it would be about the 1860's when the hedge was planted, but I cannot be sure of this - It would have been very difficult to have brought plants from, say, Sydney, in the early days - I do not know, either, where the plants were obtained - There were nurserymen in Sydney & I presume that is where the aspens, oaks, chestnuts, elms & pines were obtained - Again, I do not know, when "Sheppards" was a popular firm -

As for planting & care of hawthorns - I believe the pink ones take more looking after initially, but hawthorns are well able to take care of themselves. The tiny ones certainly benefit from water in dry times but otherwise need no care

Perhaps the Mitchell Library in Sydney may have some suggestions you might follow. I haven't read Lionel Gilbert's books, either - There may be references in those are about the Botanical Gardens in Sydney. to Hawthorns

Sincerely (Miss) Alice Nivison

076 361 222

Liston N.S.W. 2372

Mr David Bass

Dear Sir

In reference to your letter in Tenterfield Star of 23rd Nov.
As a child I remember many hawthorn hedges in the Tenterfield area & any of the older residents will be able to tell you of them. One quite famous was a mixed hawthorn & japonica hedge on both sides of the Mt Lindsay Highway at Summerlad's Orchard several miles north of Tenterfield. Though it was cut out in recent years it is easily traced by suckers

When my family came to this property nearly 40 miles north of Tenterfield there was a large hawthorn tree at the sight of a previous homestead. That was 75 years ago & that tree is still going strong & much appreciated by the cattle as a dense evergreen shade. Although a deciduous type tree it is so dense & compact that it always seems to have some foliage. It is on its own out in the open paddock & completely exposed to the elements

No wonder the pioneers used quickset hedges as a supplement to the post & rail fences

Hopeing this will help you.

Sincerely

(Mrs) I Rickard

24 Ross St
Gladesville 2111
12/12/89

To David Bass

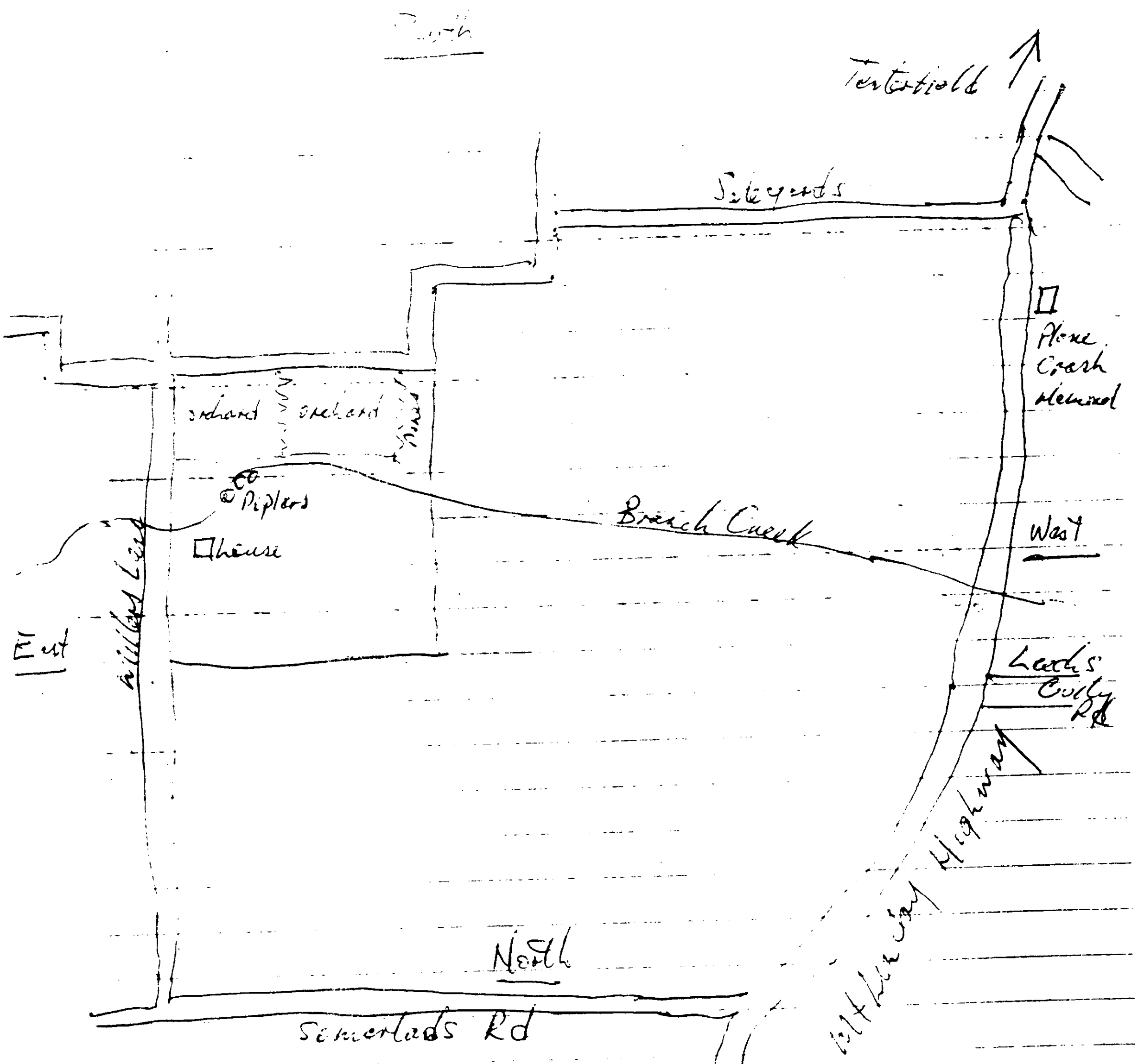
Dear Sir

I recently noted an enquiry by you on Hawthorn Hedges in the Tenterfield Star. My Grandfather Thomas Miller had protective hedges growing around his orchards which were situated about three miles north east of Tenterfield not far from the Mt Lindsay Highway. the Property was called Polar Gardens on a road now called Millers Lane. I understand that the pine trees on the westward side of the orchards were planted about 1897 and chopped down about 1950 which may give you some idea of the age of the fruit trees + hedges. I cannot give exact details of the source of the trees etc as there is a gap in our family history between 1852 and about 1880 which we are trying to trace at the moment.

My Great Grandfather Robert Miller came from Ireland in 1852 and for a time worked on Tenterfield Station which was the largest property in the Town specialising in agriculture & and animal husbandry so he would have had acess to all crops and trees brought from overseas with the early settlers. Thomas Miller corresponded with Luther Burbank according to my mother but alas all traces of such letters and replies have been lost or destroyed. I would certainly treasure such items myself today. I have included some photos which may assist you with your thesis

Yours Sincerely

Lloyd Woolnough



P.S have included rough map and suggest that you contact my cousin
Robert Miller
237 Dumaresq ST
Armidale
who may be able to help further

PTO

P.S.
I may be able to [illegible] additional notes on [illegible] 'Miller' from an article in the Tenterfield Star dated December [illegible] 1936 which was reprinted from [illegible] 1894, titled "Old Tenterfield".

If you can't get access to the above paper I may be able to copy some of it out for you.

I understand the Armidale University has collected a lot of New England history recently. It may be worth a look.

L.W.

L. & F. WOOLNOUGH
24 Ross Street
GLADESVILLE
NSW 2111

24 Ross St
Gladesville
1/3/90

to David Bass,

Sorry about not replying to your letter until now, I have been very busy. My family still feels that the source of Hawthorn Hedge cuttings would have been the "Tenterfield Station" property some time before Federation.

My nephew Dr David Murray suggests that you take care checking the growth rings on the Hawthorn as it is possible to get an incorrect result very easily.

I will be travelling through Armidale mid April, if I get a chance I will contact you.

Please keep all the photos!!

Regards
Lloyd Woolnough

read.

OLD TENTERFIELD

Reprinted from "Town and Country Journal" dated 18[illegible]4
and printed in the Tenterfield Star 31/12/1936.

There are some very fine orchards in the district including those of Mr.Thomas Miller,Mr.Sommerlad,Mr.Corrin, Mr. Corcoran Mr.Leech, Mr. Peberdy,Mr. Stewart and Mr. Arthur .

Mr.Thomas Miller,s'POPLAR GARDENS" are situated about three miles in a North Easterly direction from Tenterfield and includes an orchard of 17 acres. The fruit trees were selected by Mr. Miller with the greatest care and in every case where a tree shows signs of blight the branches were cut off and blight proof varieties grafted ons so that now, with few exceptions every tree is perfectly free from blight.

Such fruits as apples ,peaches ,plums, apricots, figs, cherries, pears, almonds and walnuts are produced here in the very highest degree of perfection. Mr. Miller recently showed some unripe cooking pears which turned the scale at 2-1/2 lbs. each also some Lord Nelson apples which weighed 1-1/4 lbs. each.

The other improvements on this property comprise a most comfortable dwelling house with kitchen and offices , large fruit store with racks and a barn and stable. A pretty flower garden and some fine ornamental trees surround the residence which stands on a very picturesque spot.

Mr. Miller may be said to be the founder of the fruit growing industry in Tenterfield. His commendable enterprise and its success has had the effect of inducing others to follow in his footsteps and now there are over 200 acres in fruit trees in the district.

Five acres of Mr. Miller's are 16 years old, the remainder with the exception of about 2 acres is 6 years old. Mr. Miller has taken innumerable prizes for his fruits at Tenterfield and other shows.

The remaining portion of this land, about 120 acres is subdivided into 10 acre cultivation and grass paddocks.

Two rows of ornamental trees are planted at regular intervals around the whole of the property, which as well as being pleasing to the eye, serve a very useful purpose by sheltering the orchard and the garden from the strong South, South-West and West winds.

Mr. Miller has been 31 years in Tenterfield.

This puts Poplar Garden orchards at c. 1878 to 1888

The article above may give you some help re the background of Thomas Miller
Please excuse the typing
Regards
Lloyd Wedlock

13/2/94
24 Ross St
Gladesville
2111

Dear David,

I have managed to gather together some information for you which may help. I would say that between 1863 and 1873 when Thomas Miller married he would have had to cleared the land, planted the orchards and built a house to live in plus barns and stables etc. As regards the Hawthorn Hedges whether they were planted at the same time as the orchard or later would only be a guess. Experience would have told him about the cold westerly winds during winter and the need to protect his plants and crops.

Kind regards,
Lloyd Woolnough.

These notes were sent to me by my cousin Gwenda Woolnough which I think should help you.

also Thomas Miller took up the Poplar Farm site in 1863 he would have been 15 – 17 years old he purchased adjacent block from his brother John who moved about a mile east to Willow Farm originally owned by Mr Goldart.

1887 Thomas Miller planted pine trees on the western sides of three orchards as further protection. These were cut down about 1950.

Thomas and John's father Robert Miller purchased land in Riley ST soon after the 1854 release as mentioned in "Historic Tenterfield" and lived there while he worked on Tenterfield Station.

Lloyd Woolnough
2/94

MEN OF MARK –

Thomas Miller – b County Down Ireland 1848, came to Colony 1852
1863 took up the 'Poplar Farm' of 135 a.

" Amongst the Orchards" 5 Nov 1898
Pines planted about 11 years ago as wind break → 1887
and is further protected by high hedges of Hawthorn &
Ossage Orange → possibley planted 1863 – 1868 L.W.

Mr Miller came to the Tenterfield district when 6 yrs old
& Has resided here ever since – he started farming on a
40 acre block (purchased) 1863 forming part of his present property
and a couple of years or so after laid foundations of his
fine orchard of today (this was some 30 yrs ago)
35 ? LW

note John Miller regretted the fact that he did not plant pinus insignis
around his orchard as the hawthorn hedge was not sufficient.
((the original grantee was Mr Geldart) John having sold his original block to
Brother Thomas)

1958 map shows –
General Cemetery dedicated 2 Mar 1873

John Henry Sommerlad
Purchased 400 a. from John Connolly at Leech's Gully 1877

Robertson Land Act 1861 able to select from 40 to 320 a anywhere
from proclaimed Crown Lands.
1862 First year 15 selectors – by 1878 nearly 1200 Selectors

Bernard Donaghey first Selector
40 acres CP 62/2568 on 20 May 1862 (possibly Portion 91)

This from Map which has R. Miller crossed out Town of Tenterfield County Clive Parish Tenterfield District of New England
First Suburban Lots – Sale at Tenterfield on 20th Nov 1857
(Lots 17 to 58)
Sale at Tenterfield 18 August 1859 – Suburban Lots 1 to 7.
Allots 3 4 Sn ~~lots~~ 4 Sns 17, 25. 52 & 1 Sn 54

Parish Map of Tenterfield dated 1958 (yes 1958) as far as I can see would have been reproduced over the years with different editions

APPENDIX 2

This appendix provides a summary of the data of J.M.B. Smith of naturalized woody plants > 1 m tall from six sites in and around Armidale. Each genera/species is expressed as a percentage of the total alien woody flora at each site. I extracted the data relating to the major genera/species used in Figs 5.6 and 5.7. Three other sites located some distance form Armidale were not used.

Site	1	2	3	4	5	6			
	214	225	211	203	214	245	204	208	230
Cytisus scoparius	–	–	–	–	–	–	–	–	3.7
Cotoneaster franchetii	–	–	0.4	–	–	2.0	–	–	–
Cot. glaucophyllus	1.0	–	–	–	2.6	13.3	–	–	–
Cot. granatensis	–	–	3.4	–	–	2.1	–	–	–
Cot. lacteus	–	–	–	–	–	11.0	–	–	–
Cot. pannosus	2.0	–	0.4	3.2	0.5	2.6	–	–	0.4
Crataegus monogyna	9.2	7.5	53.0	3.0	3.3	2.8	11.2	41.3	37.8
Cr. phaenopyrum	5.1	–	–	–	–	–	–	–	–
Ligustrum lucidum	1.4	0.4	0.5	1.9	63.6	11.9	–	–	0.4
Lig. sinense	6.5	74.1	–	1.1	3.7	–	–	1.0	1.3
Lig. vulgare	–	–	–	–	0.5	–	–	–	–
Lonicera japonica	1.4	–	–	–	1.4	0.3	–	0.5	–
Lycium ferocissimum	1.0	–	–	0.4	–	–	–	–	0.4
Malus domestica	11.9	1.3	6.4	0.8	3.3	0.3	76.3	40.4	30.0
Pinus radiata	–	1.8	–	–	–	35.1	–	0.5	12.6
Pyracantha angustifolia	30.0	–	4.6	22.3	5.1	7.0	3.0	2.9	0.9
Py crenulata	1.7	11.8	–	2.6	4.2	2.0	0.3	0.5	–
Py cf. rogersiana	11.6	–	2.6	37.0	1.9	3.5	–	–	0.9
Prunus cerasifera	6.1	0.4	0.9	1.9	1.9	–	3.3	3.4	3.5
Pr. persica	0.3	–	–	0.8	–	–	2.0	1.9	3.5
Rosa rubiginosa	10.9	–	28.3	27.2	2.8	1.7	–	–	–
Fraxinus sp.	–	2.6	–	–	–	–	–	–	–
Pistacia chinensis	–	–	0.5	–	1.4	–	–	–	–
Pyrus communis	–	–	0.5	–	–	–	0.7	0.5	–
Hedra helix	–	–	–	–	0.5	0.3	–	–	0.4
Jasminum sp.	–	–	–	–	0.5	–	–	–	–
Photinia sp.	–	–	–	–	–	0.3	–	–	–
Prunus avium	–	–	–	–	–	–	0.3	–	1.3
Prunus armeniaca	–	–	–	–	–	–	1.0	1.9	3.4
Celtis laevigata	–	–	–	–	–	–	–	4.8	–
Prunus salicina	–	–	–	–	–	–	–	0.5	–
Pinus [illegible]	–	–	–	–	–	–	–	–	0.4
Juniperus sp.	–	–	–	0.4	–	–	–	–	–

APPENDIX 3

For interest in the security of my data all relevant data has been summarised and included in tabulated form within the body of the text. The original 'raw' data is held by me and is available on request.