

RELATIVE INVASIVENESS OF TWO WOODY WEEDS IN NORTHERN NEW SOUTH WALES

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Summary This paper examines the relative invasiveness of two woody weeds; *Crataegus monogyna* and *Prunus mahaleb*. The species are closely related and have similar habits and overlapping home ranges in Europe. *C. monogyna* was introduced to Australia mainly as an ornamental and hedge plant with extensive plantings throughout southern Australia. *P. mahaleb* was introduced as rootstock for orchard trees and has only one recorded infestation in Australia. The project was focused at Armidale on the northern tablelands of New South Wales. *C. monogyna* is very invasive in the region, having spread rapidly and conspicuously throughout northern New South Wales and elsewhere in southern Australia at rates of 80–120 m y⁻¹. *P. mahaleb* is far less invasive, being restricted to a small and slowly expanding population near Armidale at 20 m y⁻¹. Demographic analysis based on three years of data coupled with modified Leslie matrices showed that potential growth rates (as expressed as the dominant latent root of transition matrix) of *P. mahaleb* (1.713–1.490) are greater than those for *C. monogyna* (1.138–1.103). Assessment of the seed dispersal ecologies of both species revealed that *C. monogyna*, an autumn-winter fruiting species, had seeds dispersed by pied currawongs over many kilometres. *P. mahaleb*, a summer fruiting species had seeds dispersed predominantly by noisy friarbirds over distances generally less than 100 m. Both plants also have seeds dispersed by an array of other vertebrates including small birds, brush-tailed possums, macropods, foxes and rabbits.

The main factors determining the difference in invasiveness between the two species are:

1. *C. monogyna* was widely and extensively planted in hedges and gardens which provided many foci for further and accelerated spread facilitated by vertebrate seed dispersal.
2. *P. mahaleb* was not planted widely and as result spread relatively slowly from a single focus.
3. Despite a more rapid population growth rate *P. mahaleb* only had seeds dispersed relatively short distances compared to *C. monogyna* which has seed dispersed over many kilometres.

This research has implications for the prediction and management of biological invasions and emphasises the importance of seed dispersal and human activities in determining the course of invasions.

INTRODUCTION

Biological invasions occur 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). Whether natural or influenced by humans, biological invasions are responsible for and ultimately change regional biotas. In order to understand the process of invasion and manage vegetation change the factors influencing the course of biological invasions need to be adequately understood. Traditional research into what determines invasiveness has focused on biological attributes of the invader (Roy 1990) and attributes of the

Table 1. Attributes of invading plants that are likely to differ with different degrees of invasiveness.

Attribute	Less invasive	More invasive
Rate of spread	Slower	Faster
Human influence e.g. active planting and propagation	Less e.g. few plantings, more horticultural management	More e.g. many plantings, abandoned plantings
Population growth rate	Slower e.g. slow growth, lower fecundity, higher mortality	Faster e.g. fast growth, higher fecundity, lower mortality
Interaction with invaded environment e.g. seed dispersal	Simple, few interactions e.g. few seed dispersers, short distance seed dispersal	Complex, many interactions e.g. many seed dispersers, long distance seed dispersal

invaded environment (Holdgate 1986, Newsome and Noble 1986). Table 1 shows some of these attributes likely to differ between species with differing invasiveness. Unfortunately the search for generalizations has in the main been unsuccessful. An avenue of research under utilized is that of comparing closely related species that differ in their degree of invasiveness (Groves 1986, di Castri 1989). This approach minimizes many of the confounding factors thereby allowing identification of the more important determinates of invasiveness.

Two closely related invading fleshy fruiting plants that differing in their invasiveness are *C. monogyna* and *P. mahaleb* which are invading on the northern tablelands of New South Wales. Both species are native to Europe where they co-occur. They are deciduous fleshy fruiting shrubs growing to seven metres. *C. monogyna* is locally very invasive having been widely planted as a hedge plant for protection of orchards, fencing, and as an ornamental plant. On the other hand *P. mahaleb*, introduced primarily as rootstock for orchard trees, occurs as a small slowly expanding population.

The study had three main foci:

- calculating rate of spread,
- modelling the rate of population growth, and
- documenting the seed dispersal ecology of both species.

MATERIALS AND METHODS

Rate of spread Both *C. monogyna* and *P. mahaleb* produce well defined annual growth rings. Rates of spread were calculated by dividing the distance from each tree to the site of first introduction by the age of each tree. The invasiveness of *C. monogyna* was calculated for a discrete population centred on the town of Tenterfield. One hedge established between 1863 and 1890 was used as the site of first introduction.

Prunus mahaleb occurs as a small (<2 km wide) slowly expanding population centred on the *Pinus radiata* dominated Armidale State Forest. The forest dates from 1916. Only the largest *P. mahaleb* trees at the extremities of the population range were felled and aged.

Population growth rates Annual censuses (1987, 1988, 1989, 1990) were made in permanent quadrats at two sites. Each species population was modelled using modified Leslie transition matrices (Burns and Ogden 1985, Caswell 1989). The dominant latent root of the transition matrix yields the finite rate of natural increase which is related to the intrinsic rate of natural increase r such that:

$$r = \ln \lambda$$

where \ln is the natural logarithm. When $\lambda < 1$ the population is in decline, $\lambda = 1$ the population is stable, and $\lambda > 1$ the population is expanding.

The first analysis utilized six height categories (0–100 cm, 100.1–200 cm, 200.1–300 cm, 300.1–400 cm, 400.1–500 cm, >500 cm). The second analysis divided the population into eight basal circumference classes (0–5, 5.1–10, 10.1–15, 15.1–20, 20.1–25, 25.1–30, 30.1–35, >35 cm) plus a seedling class (0–100 cm height). The fecundity of each size class was expressed in terms of seedlings produced per tree per year (Enright and Ogden 1979). Survival, growth, fecundity and transition rates for each size class were established for *C. monogyna* and *P. mahaleb*. The models were then applied to a 1.2 ha plot containing 185 *C. monogyna* plants >1 m tall and 4680 seedlings and 232 *P. mahaleb* plants >1 m tall and 490 281 seedlings.

Seed dispersal ecology Both species have seeds dispersed by vertebrates. Detailed observations of seed disperser behaviour and collection of faeces containing seeds were conducted over a three year period. *C. monogyna* and *P. mahaleb* differ markedly in their seed dispersal ecologies: *C. monogyna* is an autumn-winter fruiting species and *P. mahaleb* a summer fruiting species.

RESULTS

Maximum rate of spread for *C. monogyna* was 199 m y^{-1} and slowest 26 m y^{-1} . The most conservative measure of the mean rate of spread of *C. monogyna* at Tenterfield was 80.2 m y^{-1} . This is lower but similar to 120 m y^{-1} recorded by Smith (1982) for *C. monogyna* spreading near Glen Innes. The average rates of spread for *P. mahaleb* at the Armidale State Forest was 20 m y^{-1} .

Based on both the height and basal circumference models the projected rate of population growth rate of *C. monogyna* was lower than that for *P. mahaleb* (Table 2). Height models in both instances gave slightly higher values for λ than basal circumferences models.

The seed dispersal ecologies differed greatly (Table 3). *C. monogyna* had a seed dispersal system dominated by pied currawongs which were very abundant in the area during autumn and winter (Bass 1995). Mammals, principally brush-tailed possums, foxes and macropods also dispersed seeds. Pied currawongs dispersed seeds up to 10–15 km as they flew from town feeding areas to overnight roosts in the surrounding country. *C. monogyna* seeds were not well represented in pied currawong diets

Table 2. Population growth rates for *C. monogyna* and *P. mahaleb* for height and basal circumference models.

Model	<i>C. monogyna</i>	<i>P. mahaleb</i>
Height	1.138	1.713
Basal circumference	1.103	1.494

Table 3. Principal seed dispersal vectors and distances for *C. monogyna* and *P. mahaleb* at Armidale, New South Wales.

Dispersal vector	<i>C. monogyna</i>	<i>P. mahaleb</i>
Birds	Pied currawong	Noisy friarbird Red wattlebird Olive-backed oriole Silvereye Mistletoebird Pied currawong
Mammal	Brush-tailed possums Fox Macropod	Brush-tailed possums Fox Macropod Rabbit
Dispersal distance	0–10 000 m	0–100 m

as birds tended to feed more on *Pyracantha* and *Ligustrum*. Prior to *Pyracantha* and *Ligustrum* introductions, *C. monogyna* was likely to have been more important in pied currawong diets and hence more widely dispersed (Bass 1995).

Prunus mahaleb on the other hand had a well developed seed dispersal system with at least six major bird vectors, foxes, rabbits and brush-tailed possums. However seed dispersal of *P. mahaleb* only occurred over relatively short distances (<100 m).

DISCUSSION

This study highlights the complexities of plant invasions, in particular the unpredictable nature of the interaction between biological factors in determining degree of invasiveness. Intuitively the more invasive species should have faster rate of spread, higher rates of population growth, and better developed seed dispersal systems. In this study the more invasive *C. monogyna* had rates of spread 4–5 times greater than *P. mahaleb*. However the projected rate of population growth of *C. monogyna* is less than *P. mahaleb*. Also contrary to expectations *C. monogyna* has a more simple seed dispersal system dominated by pied currawongs. *P. mahaleb* has, by

comparison, a relatively more complex system on a par with the seed dispersal systems developed in its home range in southern Europe (Herrera and Jordano 1981, Guitian *et al.* 1992, Jordano 1994).

The disparity between expected attributes and relative invasiveness is counted by the influence of humans and the effectiveness of seed dispersal. *C. monogyna* has been widely planted thereby providing a large number of invasion foci which under a similar seed dispersal system will occupy new territories much faster than a single invasion point (Mack 1985). *P. mahaleb* on the other hand has a single point of introduction. Despite having many seed dispersal vectors, seed dispersal only occurs over short distances of <100 metres. This short distance seed dispersal does not allow *P. mahaleb* to express its demographic potential.

Table 4 summarizes the main findings of the project. Factors relating to the degree of human influence and interactions with invaded environments have more influence than rates of population growth in determining the level of invasiveness of a species (cf. Table 1).

The findings are relevant to the comparison of these two species. Confirmation of these trends with other invasive and non-invasive pairs of species is needed in order to validate the importance of humans and seed dispersal ecology in determining invasiveness. Despite this the implications for predicting what species will become invaders is obvious for some groups of plants. Of particular note are ornamental species which are actively promoted by the horticultural industry, local councils and other groups (Bass 1995). Not only does this study apply to invading ornamental species but it can also be utilized for management of revegetation programs.

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REFERENCES

- Bass, D.A. (1994). 'The invasiveness of *Crataegus monogyna* and *Prunus mahaleb*, at Armidale, New South Wales, Australia'. Ph.D. Thesis, University of New England, Armidale.

Table 4. Comparison of rate of spread, population growth and seed dispersal of *C. monogyna* and *P. mahaleb*.

	<i>C. monogyna</i>	<i>P. mahaleb</i>
Rate of spread (invasiveness)	Faster, 80–120 m y ⁻¹	Slower, 20 m y ⁻¹
Human influence	More, many points of introduction	Less, single point of introduction
Population growth	Slower	Faster
Seed dispersal	Simple vectors long-distance	Complex vectors short-distance

- Bass, D.A. (1995). Contribution of introduced fruits to the winter diet of pied currawongs in Armidale, New South Wales. *Corella* 19, 127-32.
- Burns, B.R. and Ogden, J. (1985). The demography of the temperate mangrove (*Avicennia marina* (Forsk.) Vierh.) at its southern limits in New Zealand. *Aust. J. Ecol.* 10, 125-33.
- Caswell, H. (1989). 'Matrix population models: construction, analysis, and interpretation'. (Sinauer Associates, Massachusetts).
- di Castri, F. (1990). On invading species and invaded ecosystems: the interplay of historical chance and biological necessity. In 'Biological Invasions in Europe and the Mediterranean Basin', eds. F. di Castri, A.J. Hansen and M. Debussche, pp. 1-16. (Kluwer Academic Publishers, Dordrecht).
- do Amaral Franco, J. (1968). *Crataegus* L. In 'Flora Europaea Volume 2', eds. T.G. Tutin, V.H. Heywood, N.A. Burges, D.M. Moore, D.H. Valentine, S.M. Walters and D.A. Webb, pp. 73-7. (Cambridge University Press, London, UK).
- Enright, N. and Ogden, J. (1979). Applications of transition matrix models in forest dynamics: *Araucaria* in Papua New Guinea and *Nothofagus* in New Zealand. *Australian Journal Ecology* 17, 507-20.
- Groves, R.H. (1986). Plant invasions of Australia: an overview. In 'Ecology of Biological Invasions: an Australian Perspective', eds. R.H. Groves and J.J. Burdon, pp. 137-49. (Australian Academy of Science, Canberra).
- Guitian, J., Fuentes, M., Bermejo, T. and Lopez, B. (1992). Spatial variation in the interactions between *Prunus mahaleb* and frugivorous birds. *Oikos* 63, 125-30.
- Herrera, C.M. and Jordano, P. (1981). *Prunus mahaleb* and birds: the high efficiency seed dispersal system of a temperate fruiting tree. *Ecol. Monogr.* 51, 203-21.
- Holdgate, M.W. (1986). Summary and conclusions: characteristics and consequences of biological invasions. *Phil. Trans. R. Soc. Lond.* B314, 733-42.
- Jordano, P. (1994). Spatial and temporal variation in the avian-frugivore assemblage of *Prunus mahaleb*: patterns and consequences. *Oikos* 71, 479-91.
- Mack, R.N. (1985). Invading plants: their potential contribution to population biology. In 'Studies on Plant Demography. A Festschrift for John L. Harper', ed. J. White, pp. 127-42. (Academic Press, London).
- Newsome, A.E. and Noble, I.R. (1986). Ecological and physiological characteristics of invading species. In 'Ecology of Biological Invasions: an Australian Perspective', eds. R.H. Groves and J.J. Burdon, pp. 1-19. (Australian Academy of Science, Canberra).
- Roy, J. (1990). In search of the characteristics of plant invaders. In 'Biological Invasions in Europe and the Mediterranean Basin', eds. F. di Castri, A.J. Hansen and M. Debussche, pp. 335-52. (Kluwer Academic Publishers, Dordrecht).
- Smith, J.M.B. (1982). 'Establishment of exotic woody plants along roadsides in New England (New South Wales)'. (Department of Geography, University of New England, Armidale).
- Webb, D.A. (1968). *Prunus* L. In 'Flora Europaea Volume 2', eds. T.G. Tutin, V.H. Heywood, N.A. Burges, D.M. Moore, D.H. Valentine, S.M. Walters and D.A. Webb, pp. 77-80. (Cambridge University Press, London, UK).