Trends in invasion by alien woody plants of the New England region, New South Wales

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Summary

Rural roadsides in New England and six sites in the city of Armidale were surveyed for alien woody plants at intervals of 18 and 13 years respectively. Sixty-three alien woody plant species were recorded in total. In the roadside study, of the 21 species recorded at least ten times at either survey time, 15 increased their populations and range and only four became less common. In the city study, the number of species recorded increased from 26 to 30, with seven species appearing and three disappearing from the sites between surveys; of 23 species recorded at both survey times, 11 increased and only two decreased in number of sites occupied. Species whose seeds are bird-dispersed were prominent, particularly among those whose invasions appeared most advanced. By contrast, wind-dispersed species were fewer, concentrated in the category of recent invaders, and apparently remaining longer as 'sleeper' weeds. The surveys document the accelerating scale of invasion of the region by alien woody plants.

Introduction

Most alien plant species in Australia were introduced during the last 212 years, since European settlement, a period that for woody plant species represents just a few generations. Humphries *et al.* (1991) have defined a naturalized plant species as 'an invading species that has become established and has reproduced for several generations in the wild'. By such a definition, barely enough time has elapsed for most alien woody species to become truly naturalized.

There may be a prolonged lag between a plant's initial introduction to an area and the start of any subsequent invasion (Hobbs and Humphries 1995, Wade 1997). Species suspected of being in an invasion lag phase are commonly referred to as 'sleepers' (Humphries *et al.* 1991). Kowarik (1995) examined biological invasions by woody plants of Brandenburg, Germany, over five centuries, and showed that 'only 6% of the 184 species (which eventually invaded) began to spread within 50 years after their first cultivation, 25% lagged up to 100 years, 51% up to 200 years, 14% up to 300 years and 4% invaded only after more than three centuries'. Invasive shrubs (including lianes) began to spread after, on average, 131 years, and trees after 170 years, with only 7.4% of all introduced woody species having demonstrated invasiveness by 1995. There was no relationship between duration of the lag phase and ultimate invasion success. Kowarik concluded that 'the number of invasions breaking out will increase, even if no additional species are introduced'. He also found that invasion once started was not inexorable, and about as many species became extinct after having begun to invade, as went on to become members of 'natural' vegetation.

Such experience implies that, in Australia, many woody plants introduced even early in European settlement are likely only now (or not yet) to be starting to invade local environments. It is also clear that most woody species already behaving invasively in Australia have not yet occupied their full potential ranges, being confined to only small parts of their regions of suitable climate, or clustering around towns where parental plants have been introduced. The scale of invasion of Australian environments by alien woody flora is increasing rapidly (Groves and Hosking 1997). Yet, while there is awareness of this, most Australian studies have focused on 'snapshot' views of regional invasion patterns, or on single species of invading plant. There is a dearth of studies upon the invasion of regions by suites of alien species over periods spanning a decade or longer.

The results of two such studies, spanning 18 and 13 years, of alien woody plants (trees, shrubs and woody lianes) in the New England region of New South Wales are presented here. The first study was a survey of the flora of rural roadsides first conducted in December 1980 and repeated in January 1999. The second study was a survey of six sites at Armidale city first conducted in October 1986 and repeated in October 1999.

Plant nomenclature follows Harden (1990-93) wherever possible, and as below for species not included therein: *Cotoneaster lucidus* Schtdl., *Crataegus phaenopyrum* (L.f.) Medik., *Fraxinus angustifolia* Vahl, *Juglans regia* L., *Pinus ponderosa* Douglas ex Lawson & C.Lawson, *Populus tremula* L., *Pyrus communis* L., *Quercus palustris* Munchh., *Quercus robur* L., *Syringa vulgaris* L., *Ulmus parvifolia* Jacq., *Ulmus procera* Salisb., *Vitis vinifera* L. Specimens of most plant species listed here are lodged in the University of New England herbarium (NE), including the following specimens of unidentified plants: *Cotoneaster* sp. JMBS 975, *Cupressus* sp. JMBS 995, *Sorbus* sp. JMBS 992.

The rural (roadside) study

The 1980 survey

In December 1980, a survey was conducted of New England rural roadsides (Smith 1982a,b). The study region extended to near Tenterfield in the north, to Nemingha (near Tamworth) and Walcha in the south-west, to Gibraltar Range and Dorrigo in the east, and to Inverell and Kingstown in the west (Figure 1). Altitudes range from more than 1200 m in the central Guyra-Glencoe area, to below 800 m in the Inverell-Tingha, Kingstown and Nemingha areas to the west of the tableland and in the Dorrigo-Bostobrick area to the east. Temperatures vary inversely with altitude, and climates are moister in the east and drier in the west of the study region. The study was mainly confined to the Northern Tablelands botanical region of New South Wales, but extended slightly into the North-west Slopes region in the Inverell and Nemingha areas, and the North Coast region in the Dorrigo-Bostobrick area.

Several taxa in the 1980 survey appeared to be restricted within the region by climatic factors. *Ligustrum lucidum* and *L. sinense* were most abundant in warm, moist areas in the east of the study region; *Ailanthus altissima* and *Prunus persica* were commonest at lower altitudes; *Pinus radiata* and *Pyracantha angustifolia* were commonest in moister areas; *Malus domestica*, *Populus* spp., *Ulmus procera*, *Crataegus monogyna*, *Cotoneaster* spp. and *Pyracantha* other than *P. angustifolia* were commonest on the tableland; *Cytisus scoparius* occurred mainly at the highest altitudes; while *Prunus armeniaca*, *P. cerasifera*, *Pyrus communis* and *Robinia pseudoacacia* were widespread.

Overall, the commonest species were, in order, *Malus domestica*, *Crataegus monogyna*, *Prunus persica*, *P. cerasifera*, *Ligustrum sinense*, *Ulmus procera*, *Populus nigra* (especially cv. 'Lombardy') and *Pinus radiata* (Table 1). Fruit tree numbers varied with traffic volume, indicating that these plants were predominantly derived from fruit wastes discarded from vehicles (Smith 1982a,b). Fleshy-fruited ornamental shrubs occurred particularly near towns, a pattern emphasized also in a similar, subsequent study extending beyond the region (Smith 1985), reflecting the garden locations of parental individuals of those species.

Methods

In 1999 the rural survey was repeated using the same methodology as in 1980, in

order to discover changes in abundance and diversity in the alien woody flora after a lapse of 18 years. The same roads were surveyed, although some had changed in detail due to road improvements, alteration of speed limit zones, etc. Data were collected from a slow-moving vehicle using a hand-held tape-recorder, altogether covering 1193 km of road located outside urban speed restriction zones. Wild (unplanted) alien woody plants and lianes taller than one metre were recorded to either side of the road up to 15 m from the road edge, or up to the roadside fence if that was closer. If more than 10 individuals of a species were counted per kilometre of road the species was noted as abundant and not counted further, except for fruit trees all of which were counted. A driver other than the recorder was used for most roads, including all the busier ones.

Following the earlier survey, some taxa were ignored for various reasons: *Genista monspessulana*, *Ligustrum vulgare*, *Rosa rubiginosa* and *Rubus fruticosus* agg. (all commonly shorter than one metre, the last two commonly controlled by herbicide spraying), *Salix babylonica* (apparently usually planted), *Cinnamomum camphora* and *Solanum mauritianum* (restricted to the south-eastern extremity of the study region), *Acacia farnesiana* (arguably native) and species native to other regions of Australia including *Acacia baileyana*, *Grevillea rosmarinifolia* and *Melia azederach*. Species of *Cotoneaster* and plums (*Prunus cerasifera*, *P. domestica*, *P. salicina*) were not consistently distinguished in the earlier survey but were so in the later one. Species of *Pyracantha* other than *P. angustifolia* (*P. crenulata*, *P. rogersiana* and possibly *P. fortuneana*), and of *Pinus* other than *P. radiata*, were not distinguished in either survey. Counts of *Populus alba* and *P. nigra* included their columnar cultivars 'Pyramidalis' ('Bolleana') and 'Lombardy' respectively.

The methodology aimed at rapid accumulation of large amounts of data from a wide region, rather than focusing on detailed information from a smaller area. It was apparent that due to visibility problems (e.g. small individuals located down banks or behind larger plants) and difficulties in quickly recording large amounts of data, some plants were probably not recorded. As a check on the magnitude of this problem, two lengths of road (Castledoyle, Guyra-Armidale) were surveyed twice, in opposite directions. It was found that no species, but up to a third of individuals of some commoner species, were missed on one of the two traverses of the same road. Small recorded changes in abundance between the surveys may therefore be artefacts of the methodology adopted, and only large changes are discussed below.

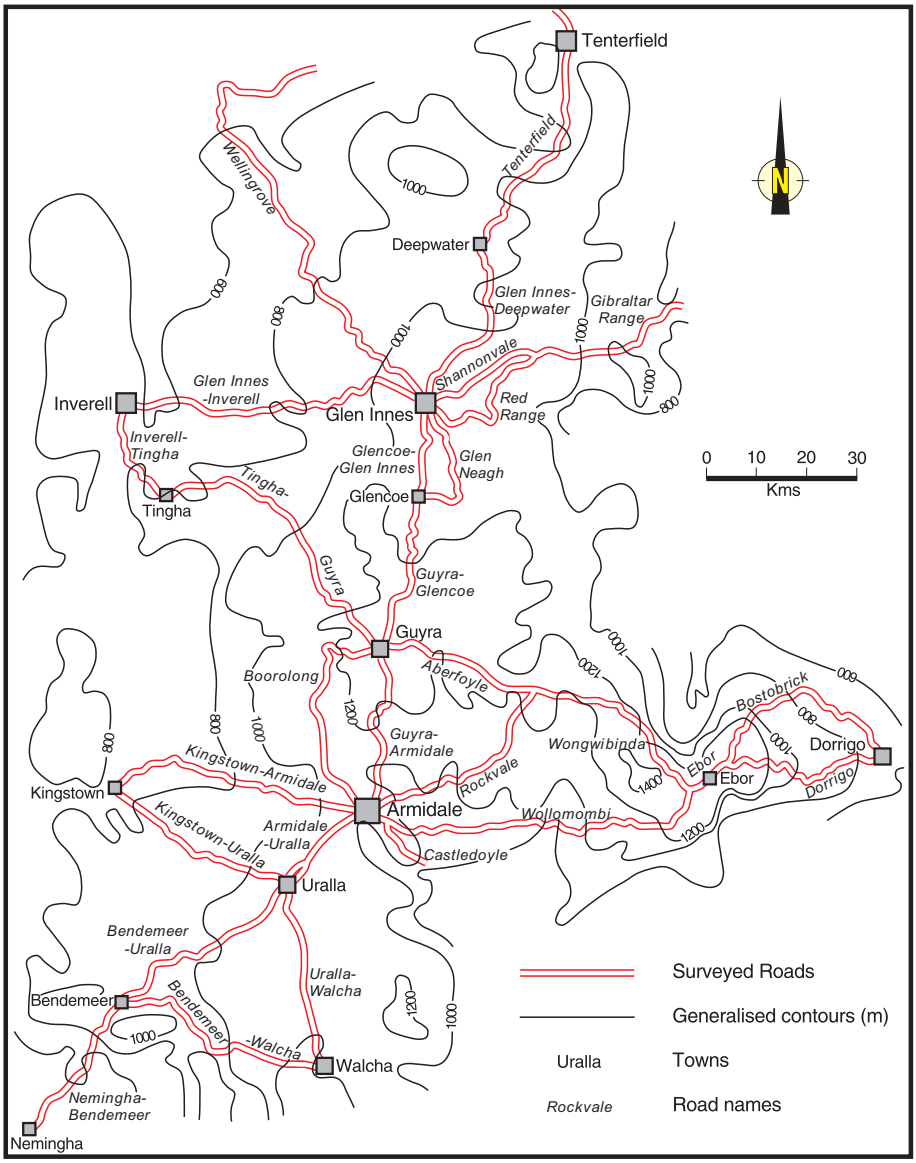

Figure 1. Roadsides surveyed in 1980 and 1999.

Table 1. Rank order of abundance of rural roadside taxa in 1980 and 1999.

Taxon	1999 ranking (road km)	1980 ranking (road km)
Malus domestica	1 (548)	1 (500)
Crataegus monogyna	2 (277)	2 (223)
Prunus cerasifera	3 (115)	4 (c. 100)
Pyracantha angustifolia	4 (105)	15 = (15)
Populus nigra	5 (94)	5 (64)
Pinus radiata	6 (93)	7 (50)
Prunus persica	8 (74)	3 (107)
Ligustrum sinense	9 (67)	6 = (56)
Ulmus procera	10 (48)	6 = (56)
Pyracantha spp. al.	11 = (37)	10 (34)
Populus alba	11 = (37)	13 (22)
Prunus armeniaca	13 (27)	11 (32)
Cotoneaster glaucophyllus	14 = (26)	19 (c. 4)
Pyrus communis	14 = (26)	12 (25)
Robinia pseudoacacia	14 = (26)	14 (20)
Lonicera japonica	17 (21)	– (2)
Cotoneaster pannosus	18 (20)	– (c. 2)
Cotoneaster spp. al.	19 (17)	– (c. 2)
Ailanthus altissima	20 (15)	15 = (15)

Results

Abundances in both surveys of all those taxa recorded at least ten times in at least one survey are presented in Table 2. Data for fruit trees are for all individuals; for other taxa data are for number of kilometres of roadside at which the plants were recorded. The data are presented for four climatic categories, with the 'warm moist' category comprising the Bostobrick and Dorrigo roads; 'warm dry' comprising the Wellingrove, Glen Innes-Inverell, Inverell-Tingha and Nemingha-Bendemeer roads; 'cold' comprising the high altitude roads in the Guyra-Glencoe area (Glen Neagh, Glencoe-Glen Innes, Guyra-Glencoe, Booroolong, Guyra-Armidale, Aberfoyle and Wongwibinda roads); and 'cool' comprising all remaining roads. This division is somewhat arbitrary but serves to reveal general trends for some taxa whose establishment appears to be strongly influenced by climatic factors.

Of the 21 taxa (combining species of *Cotoneaster* and plums, as was done in the earlier survey) included in Table 2, fifteen increased their overall populations, two were unchanged, and only four decreased. Thirteen significantly (>120%) increased their populations, and seven recorded increases exceeded 200%: *Populus alba*, *Prunus cerasifera*, *Ligustrum lucidum*, *Cotoneaster* and *Lonicera japonica* did so generally throughout the study region, while *Pyracantha angustifolia* and *Hedera helix* did so especially in cooler areas. Just two species significantly decreased in population: that of *Prunus persica* fell to 60%, the main drop occurring in cooler areas, and *Cytisus scoparius* disappeared from roadsides altogether probably as a result of vigorous weed control programs in recent years.

Ranked order of the commonest taxa (here separating species of *Cotoneaster* and plums, using approximate figures for 1980; and for all taxa using number of kilometres of roadside occupied) are given in Table 1. *Pyracantha angustifolia*, *Lonicera japonica* and species of *Cotoneaster* climbed markedly in rank order over the 18 year period between the surveys, evidently being the most rapidly invading species at the regional scale. By contrast, *Prunus persica*, *Ligustrum sinense*, *Ulmus procera* and *Ailanthus altissima* conspicuously dropped in ranking, although only the first of these suffered a significant fall in absolute numbers.

Several less common taxa also increased their populations beside roads between the two surveys, including *Cydonia oblonga*, *Pinus* other than *P. radiata*, *Quercus palustris* and *Salix cinerea*, recorded beside fewer than 10 km of road but increasing previous recorded populations by >200%. *Celtis australis*, *Maclura pomifera*, *Prunus cerasus* and *Schinus areira* showed little change, *Gleditsia triacanthos* dropped from five occurrences to one, and the local and rare species *Lycium ferocissimum*, *Syringa vulgaris* and *Ulex europaeus* disappeared. Outnumbering these were newly invading species, not noted at all in 1980 and occupying fewer than 10 km of roadside in 1999: *Cupressus* sp. 995 (beside 4 km of road, in widely separated places); *Acer negundo* (3 km, also widely separated); *Bambusa* sp., *Juglans regia*, *Morus alba*, *Prunus mahaleb* and *Ulmus parvifolia* (2 km each); and *Chaenomeles japonica*, *Crataegus phaenopyrum*, *Fraxinus angustifolia*, *Ilex aquifolium*, *Olea europaea*, *Passiflora mollissima*, *Pistacia chinensis*, *Populus tremula* and *Quercus robur* (1 km each).

General observations of roadsides in the region made between the two survey periods did not suggest that management of roadside plants had changed to any great extent or had strongly influenced overall patterns in alien plant establishment or persistence. Removal of roadside fruit trees occurred sporadically, and *Cytisus scoparius* and possibly *Lycium ferocissimum* (as well as *Rosa rubiginosa* and *Rubus fruticosus* agg.) were more consistently targeted for herbicidal treatment. Otherwise, individual roadside woody plants generally appeared to have been removed only as part of other operations such as road widening. Such operations did not appear to have been the cause of major new infestations by alien woody flora.

Table 2. Changes in abundance on rural roadsides (in climate categories) of taxa recorded more than ten times in either roadside survey; 1999 data, with 1980 data in parentheses.

Fruit trees (individuals)	Warm moist (88 km)	Warm dry (221 km)	Cool (638 km)	Cold (246 km)	All roads (1193 km)
Malus domestica	64 (75)	110 (105)	1090 (854)	449 (305)	1713 (1339)
Prunus spp. 'plums'	14 (3)	20 (17)	262 (53)	99 (45)	395 (118)
Prunus persica	15 (15)	47 (52)	29 (75)	7 (21)	98 (163)
Prunus armeniaca	– (–)	17 (6)	14 (27)	5 (9)	36 (42)
Prunus avium	1 (–)	1 (–)	8 (1)	8 (1)	18 (2)
Pyrus communis	– (–)	2 (4)	6 (9)	23 (18)	31 (31)
Other taxa (road km)					
Crataegus monogyna	3 (1)	15 (17)	174 (89)	85 (116)	277 (223)
Populus alba	1 (–)	3 (–)	26 (14)	18 (8)	48 (22)
Populus nigra	– (–)	14 (3)	57 (46)	23 (15)	94 (64)
Pyracantha angustifolia	2 (2)	12 (2)	70 (2)	21 (9)	105 (15)
Pinus radiata	8 (11)	7 (2)	69 (28)	9 (9)	93 (50)
Ligustrum lucidum	21 (16)	29 (8)	21 (9)	7 (4)	78 (37)
Ligustrum sinense	45 (47)	2 (1)	13 (4)	7 (4)	67 (56)
Cotoneaster spp.	3 (–)	7 (1)	37 (6)	16 (1)	63 (8)
Ulmus procera	– (–)	8 (5)	24 (26)	16 (25)	48 (56)
Pyracantha spp. al.	1 (–)	1 (–)	24 (30)	11 (4)	37 (34)
Robinia pseudoacacia	2 (1)	9 (3)	13 (13)	2 (3)	26 (20)
Lonicera japonica	7 (–)	1 (–)	11 (2)	2 (–)	21 (2)
Ailanthus altissima	– (–)	11 (10)	4 (5)	– (–)	15 (15)
Hedera helix	3 (–)	– (–)	2 (2)	6 (1)	11 (3)
Cytisus scoparius	– (2)	– (1)	– (4)	– (4)	– (11)

The city (Armidale) study

Methods

This study was of sites in and near Armidale city, in proximity to gardens which appear to be the major source of invasive woody plants (Blood 1999). It therefore complements the roadside study which was restricted to rural areas. Six sites were studied in October in both 1986 and 1999 (Figure 2). Sites 1 and 5 were adjacent to suburban gardens, Sites 3 and 6 were within one hundred metres of landscaped, planted areas of university gardens, while Sites 2 and 4 were approximately 4 km and 1 km away, respectively, from large areas of suburban gardens. No significant changes in condition or management of the sites occurred between the surveys.

1. **Erskine Street.** Small, east-facing valley grazed by horses, nearly surrounded by suburban gardens; grassland with scattered eucalypts and many small alien trees; colluvium and clay soil on basalt.
2. **Pine Forest.** Level section of Armidale State Forest planted with pines and some deciduous trees; lightly grazed by cattle, used extensively by recreationists and close to a winter roost of pied currawongs which carry seeds from Armidale (Bass 1990); alluvium.
3. **Boilerhouse Hill.** Area of degraded eucalypt forest on south side of hill at northern edge of University of New England campus; clay soil on basalt.

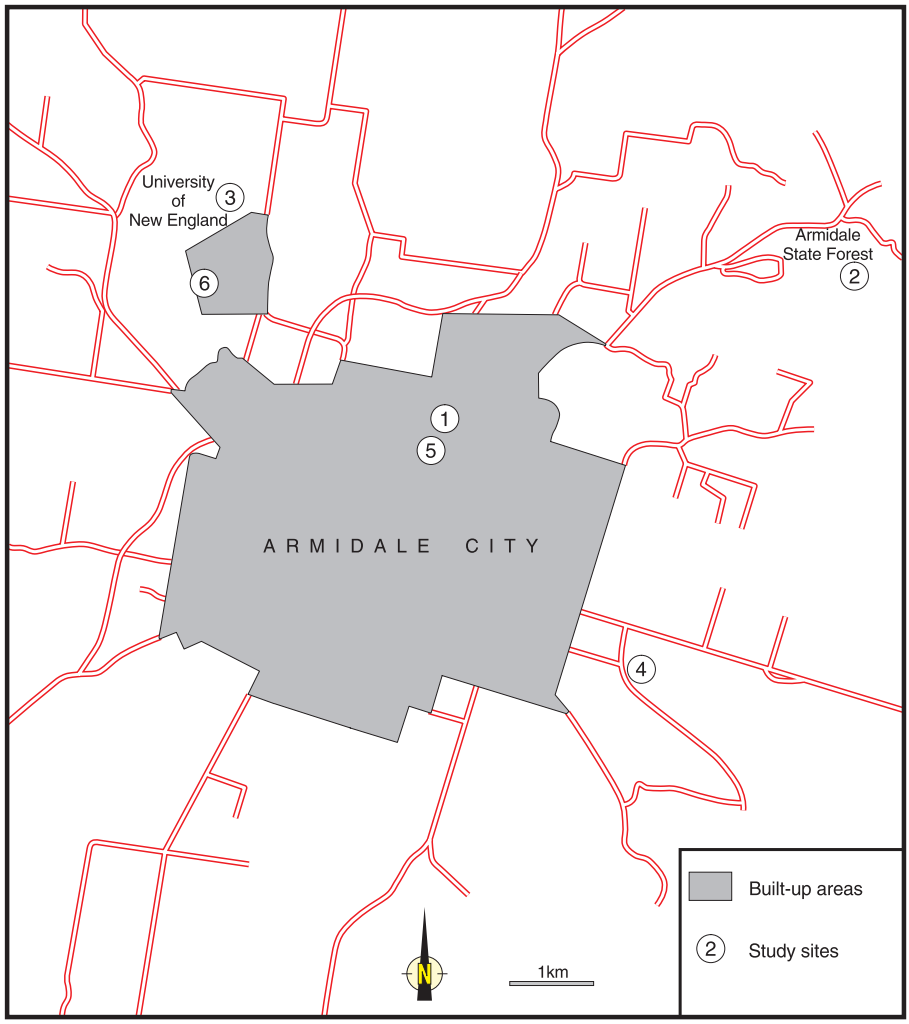

Figure 2. Locations of survey sites in the city of Armidale), 1986 and 1999.

4. **Mann Street.** Area of regenerating eucalypt woodland in travelling stock reserve on west-facing slope at the east edge of the city; sandy soil on metasediments.
5. **Apex Lookout.** Degraded eucalypt woodland on hilltop, with suburban gardens to the east, and parks and paddocks on the other sides; clay soil on basalt.
6. **Economics Hill.** Area of regenerating eucalypt woodland invaded by large pines, on south-facing slope near the western edge of University of New England campus, evident heavy macropod browsing in 1999; shallow sandy soil on metasediments.

At each site on each occasion, the first *c.* 200–500 individual alien woody plants (including lianes) taller than one metre that were encountered during a slow walk were recorded. The scarcely woody *Rubus fruticosus* agg., suckering trees (*Populus alba, P. nigra, Robinia pseudoacacia, Ulmus procera*), *Genista monspessulana* (overwhelmingly abundant in part of Site 5 but absent elsewhere) and species native to other regions of Australia (*Acacia baileyana, Grevillea rosmarinifolia, Livistona australis*, all rare) were not counted. *Rosa rubiginosa* was initially included, but later removed from the data set when it was found that its abundance by 1999 had been drastically reduced by herbicide spraying at both sites where it had been common in 1986. All species of *Cotoneaster*, *Pinus* and *Pyracantha* were distinguished. Some results from the 1986 survey have been summarized previously by Bass (1996a).

Results

The nature of the data collected in these surveys does not allow confident evaluations of changes in absolute abundance, although the larger number of plants consistently recorded at the two dates in approximately the same areas suggests an overall increase. Overall, 33 species were recorded (Table 3). Twenty-three species were present at both survey times, seven appeared for the first time in 1999, and three disappeared. Eleven of the species present at both times were recorded at more sites in 1999, 10 species occupied the same number of sites (three being present at all six sites), and only two were recorded at fewer sites. At every site, as well as overall, more species were recorded in 1999 than in 1986. The general picture is therefore of increasing invasion.

There were significant differences between the six alien woody floras, the commonest species at Sites 1–6 being, respectively, *Pyracantha angustifolia, Ligustrum sinense, Crataegus monogyna, Pyracantha rogersiana, Ligustrum lucidum* and *Pinus radiata*. The local dominance by these species was the same in both years. In 1986, when data from all sites were combined, the commonest species overall (all with 10–14%) were *Ligustrum sinense, Crataegus monogyna, Pyracantha angustifolia, Ligustrum lucidum* and *Pyracantha rogersiana*. By 1996 the same five species remained commonest overall, but *Crataegus monogyna* increased its percentage from 13.2 to 19.6, and *P. rogersiana* increased from 10.4 to 16.2, in both cases increases occurring at all sites where the species were common. *Ligustrum sinense* dropped from 13.5 to 9.8, especially at the two sites where it was most common where grazing may have been responsible for its reduction. The other two of the five commonest species, *Pyracantha angustifolia* and *Ligustrum lucidum*, experienced both increases and decreases at individual sites and overall recorded respectively a slight increase and a slight decrease in relative abundance. *P. angustifolia* and *P. rogersiana*, present at the other five sites in 1986, were both recorded also at Site 2 in 1999.

Among the less common species, three (*Pistacia chinensis*, *Cotoneaster franchetii* and *Fraxinus angustifolia*) more than tripled their overall relative abundance, and each also appeared in 1999 at two or three sites where they had not been noted in 1986. *Lonicera japonica, Crataegus phaenopyrum* and *Cupressus* sp. 995 also showed increases in both the number of sites at which they were recorded, and in overall abundance. *Cotoneaster lacteus*, *Pinus radiata* and *Pyrus communis* were each recorded at one more site in 1999 than in 1986 but without overall increases in relative abundance. Another seven species were recorded for the first time in 1999: *Acer negundo, Celtis australis, Pinus ponderosa, Prunus armeniaca, Sorbus* sp. 992, *Syringa vulgaris* and *Vitis vinifera*.

Compared with these spreading species, only a small number of alien woody species became less widespread. *Prunus persica* disappeared from three of its former four sites, with an overall quartering of its relative abundance. *Hedera helix* disappeared from Site 5 while more than tripling its relative abundance at Site 6. *Jasminum* sp., *Ligustrum vulgare* and *Lycium ferocissimum* disappeared from the single sites where they had been rare in 1986. Seven species (*Cotoneaster lucidus, C. glaucophyllus, C. pannosus, Malus domestica, Photinia serratifolia, Prunus cerasifera, Pyracantha crenulata*) were recorded in the same number of sites with the same or a reduced relative abundance.

Table 3. Species composition (per cent) of alien woody floras at six sites at Armidale in 1986 (first value in each cell) and in 1999 (second value).

Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	All sites	No. sites
Acer negundo	–	–	–	–	–	0 / 0.4	0 / 0.1	0 / 1
Celtis australis	–	0 / 1.0	–	–	–	–	0 / 0.1	0 / 1
Cotoneaster franchetii	0 / 0.5	–	1.3 / 0.8	–	0 / 0.6	2.1 / 14.7	0.6 / 3.3	2 / 4
Cotoneaster glaucophyllus	1.1 / 0.5	–	–	–	5.8 / 2.0	13.6 / 9.8	4.1 / 2.5	3 / 3
Cotoneaster lacteus	–	–	–	–	0 / 1.6	11.2 / 8.4	2.6 / 2.1	1 / 2
Cotoneaster lucidus	–	–	1.3 / 0.8	–	–	2.9 / 1.3	0.8 / 0.4	2 / 2
Cotoneaster pannosus	2.3 / 0.3	–	1.3 / 1.1	1.0 / 2.7	0.5 / 2.2	2.7 / 0.4	1.4 / 1.1	5 / 5
Crataegus monogyna	10.3 / 12.6	7.5 / 14.1	73.9 / 86.8	4.2 / 2.7	3.4 / 7.3	5.9 / 14.0	13.2 / 19.6	6 / 6
Crataegus phaenopyrum	5.7 / 5.3	–	0 / 0.4	–	0 / 0.8	–	1.0 / 1.2	1 / 3
Cupressus sp. 995	–	0 / 2.4	–	0.5 / 1.0	0 / 0.2	–	0.1 / 0.5	1 / 3
Fraxinus angustifolia	0 / 8.9	2.6 / 2.1	0 / 0.4	–	–	–	0.4 / 1.9	1 / 3
Hedera helix	–	–	–	–	0.5 / 0	0.3 / 1.1	0.1 / 0.2	2 / 1
Jasminum sp.	–	–	–	–	0.5 / 0	–	0.1 / 0	1 / 0
Ligustrum lucidum	1.5 / 2.3	0.4 / 0.7	0.6 / 0.8	2.6 / 1.7	65.4 / 36.4	12.1 / 13.1	12.7 / 11.9	6 / 6
Ligustrum sinense	7.3 / 1.5	74.1 / 64.3	–	1.5 / 0.3	3.8 / 4.2	–	13.5 / 9.8	4 / 4
Ligustrum vulgare	–	–	–	–	0.5 / 0	–	0.1 / 0	1 / 0
Lonicera japonica	1.5 / 1.5	–	0 / 0.4	–	1.4 / 1.0	0.3 / 2.0	0.5 / 1.0	3 / 4
Lycium ferocissimum	–	–	–	0.5 / 0	–	–	0.3 / 0	1 / 0
Malus domestica	13.4 / 7.6	1.3 / 0.3	8.9 / 2.3	1.0 / 0.7	3.4 / 2.6	0.3 / 0.2	4.2 / 2.4	6 / 6
Photinia serratifolia	–	–	–	–	–	0.3 / 0.4	0.1 / 0.1	1 / 1
Pinus ponderosa	–	0 / 0.7	–	–	–	–	0 / 0.1	0 / 1
Pinus radiata	–	1.8 / 7.9	–	0 / 1.0	–	35.7 / 24.0	8.5 / 6.1	2 / 3
Pistacia chinensis	0 / 1.8	–	0.6 / 2.3	0 / 0.3	1.4 / 6.7	0 / 0.7	0.3 / 2.3	2 / 5
Prunus armeniaca	–	–	–	–	0 / 0.2	–	0 / 0.5	0 / 1
Prunus cerasifera	6.9 / 1.3	0.4 / 0	1.3 / 0.4	2.6 / 1.4	1.9 / 3.4	0 / 0.2	2.0 / 1.3	5 / 5
Prunus persica	0.4 / 0	0.4 / 0	–	1.0 / 0.3	–	–	0.2 / 0.05	3 / 1
Pyracantha angustifolia	33.6 / 31.3	0 / 0.3	6.4 / 1.1	30.6 / 29.8	5.3 / 10.1	7.1 / 4.9	13.0 / 13.1	5 / 6
Pyracantha crenulata	1.9 / 3.5	11.8 / 5.8	–	3.6 / 1.0	4.3 / 2.0	2.1 / 1.3	3.7 / 2.5	5 / 5
Pyracantha rogersiana	13.0 / 20.5	0 / 0.3	3.8 / 2.3	50.1 / 56.9	1.6 / 18.4	3.5 / 2.4	10.4 / 16.2	5 / 6
Pyrus communis	0 / 0.3	–	0.6 / 0.4	–	–	–	0.1 / 0.1	1 / 2
Sorbus sp. 992	–	–	–	–	0 / 0.2	0 / 0.2	0 / 0.1	0 / 2
Syringa vulgaris	–	–	–	–	0 / 0.2	–	0 / 0.05	0 / 1
Vitis vinifera	–	–	–	–	0 / 0.2	–	0 / 0.05	0 / 1
Total counted	262 / 393	228 / 291	157 / 266	193 / 295	208 / 506	339 / 450	1387 / 2201	

Discussion and conclusions

In Table 4, for both studies all species are categorized according to their demonstrated potential for invasion in this region.

For the rural study:

- 'increasers' are defined as species which were recorded in 1980 beside ten or more kilometres of road and which in 1999 had increased their occurrence by 120% or more;
- 'recent invaders' are species which occurred beside fewer than ten kilometres of road in 1980 (or not at all) and had increased by 1999;
- 'decreasers' are species falling in abundance ranking by three or more (see Table 1) or which disappeared altogether between surveys;
- 'unchanged' are species in none of the above categories.

For the city study:

- 'increasers' are species present in at least two sites in 1986 and found in at least the same number of sites in 1999 with an increased overall abundance;
- 'recent invaders' occurred at one or no site in 1986 and by 1999 had increased the number of sites occupied without reduction in overall relative abundance;
- 'decreasers' occurred in the same or fewer sites in 1999 than in 1986, with an overall decrease in relative abundance;
- 'unchanged' are species which increased in number of occupied sites while decreasing in overall relative abundance, or retained the same sites and abundance.

In comparing the two lists, differences in methodology must be borne in mind. Suckering species were not recorded in the city study, even though *Ulmus procera* occurred at three sites and *Populus alba, P. nigra* and *Robinia pseudoacacia* at one site, all represented by many vigorous suckers from planted parent trees. The rural study spanned a wider range of climates than the geographically restricted city study. Recorded abundances in the rural study are absolute, while in the city study they are relative. It should also be recalled that in both studies, only individuals taller than 1 m were recorded so that apparent absence by a species might have been due to the presence only of shorter individuals.

Nevertheless there are some revealing similarities. Three species (*Crataegus monogyna*, *Lonicera japonica*, *Pyracantha angustifolia*) are categorized as increasers in both studies; four species (*Acer negundo*, *Crataegus phaenopyrum*, *Cupressus* sp. 995, *Fraxinus angustifolia*) appear as recent invaders in both studies; and a further two (*Hedera helix*, *Pistacia chinensis*) are an increaser in one study and a recent invader in the other. It appears from both studies that most alien woody plants in New England are increasing their populations and ranges: only *Ligustrum sinense*, *Lycium ferocissimum* and *Prunus persica* appear as decreasers on both lists. Of these, *L. sinense* did not decline substantially in either study, while *L. ferocissimum* was initially rare in both studies and might have been eliminated by herbicide spraying.

P. persica was possibly a victim of drought mortality both in Armidale and along regional roadsides.

There are also contrasts between the two studies. Five species (*Cotoneaster glaucophyllus, C. pannosus, Ligustrum lucidum, Malus domestica, Prunus cerasifera*) are categorized as increasers in the rural study but as decreasers in the city study. This may indicate that these well established species have reached quasi-stable population levels in city environments where they have been present for many years, but are still spreading in rural areas formerly remote from seed sources. The opposite pattern, of decrease in rural areas but increase in the city, does not appear.

Also included in Table 4 is information on principal seed (or vegetative) dispersal mechanisms. Some species could be included in more than one dispersal category, for example *Lonicera japonica* and *Prunus avium* are dispersed both by birds and humans, and *Acer negundo* and *Ligustrum lucidum* may be dispersed by water as well as by other mechanisms. In all such cases a judgement has been used as to the predominant vector in this region. Most species in the 'other' category appear to be poorly dispersed, and regenerate mainly in the immediate vicinity of parent plants.

Nine of the fifteen increasers in the roadside study, and all six in the city study (67% in total), are species with small fleshy fruits whose seeds are dispersed mainly by frugivorous birds. Overall, of a total of 63 species listed, 27 (43%) are bird-dispersed. This generally agrees with results of other studies. Rejmanek (1995, 1996) noted that fleshy-fruited alien species with local vertebrate seed dispersers are very likely to be invasive. In Kowarik's (1995) German study, 10 of the 11 woody species to invade most rapidly (with lags of less than a century) were bird-dispersed. In a preliminary world survey of invasive woody plants, Binggeli (1996) found 48% of 288 invasive woody plant species, as well as 48% of 38 highly invasive species, to be bird-dispersed.

Expanding 'halos' of alien, bird-dispersed, woody plant species have previously been noted as developing around New England towns, spreading from planted ornamental specimens in gardens and along streets (Smith 1985, Smith *et al*., in press). The range of seed dispersal by the pied currawong, one of the major dispersers of fleshy-fruited plants at Armidale, has been suggested to be at least 4 km (Smith *et al*., in press) and up to 10–15 km (Bass 1996b). Some invading species are still in their first generation of spread (e.g. *Pistacia chinensis*, Smith *et al*. in press), and can be expected to invade more extensively as the first wild specimens reach reproductive maturity.

Table 4. Invasiveness of all species recorded in both studies, with indications of principal dispersal mechanisms. B – bird, W – wind, H – human, S – suckering, O – other.

	Rural (roadside) study	City (Armidale) study
Increasers	*Cotoneaster glaucophyllus* B *Cotoneaster pannosus* B *Cotoneaster* sp. 975 B *Crataegus monogyna* B *Hedera helix* B *Ligustrum lucidum* B *Lonicera japonica* B *Malus domestica* H *Pinus radiata* W *Populus alba* S *Populus nigra* S *Prunus avium* H *Prunus cerasifera* B *Pyracantha angustifolia* B *Robinia pseudoacacia* S	*Cotoneaster franchetii* B *Crataegus monogyna* B *Lonicera japonica* B *Pistacia chinensis* B *Pyracantha angustifolia* B *Pyracantha rogersiana* B
Recent invaders	*Acer negundo* W *Bambusa* sp. S *Chaenomeles japonica* S *Crataegus phaenopyrum* B *Cupressus* sp. 995 W *Cydonia oblonga* S *Fraxinus angustifolia* W *Ilex aquifolium* B *Juglans regia* H *Morus alba* B *Olea europaea* B *Passiflora mollissima* B *Pinus* spp. al. W *Pistacia chinensis* B *Populus tremula* S *Prunus mahaleb* B *Quercus palustris* O *Quercus robur* O *Salix cinerea* H *Ulmus parvifolia* W	*Acer negundo* W *Celtis australis* B *Crataegus phaenopyrum* B *Cupressus* sp. 995 W *Fraxinus angustifolia* W *Hedera helix* B *Pinus ponderosa* W *Prunus armeniaca* H *Pyrus communis* H *Sorbus* sp. 992 B *Syringa vulgaris* O *Vitis vinifera* H
Unchanged	*Celtis australis* B *Maclura pomifera* O *Prunus armeniaca* H *Prunus cerasus* S *Prunus domestica* H *Prunus salicina* H *Pyracantha* spp. al. B *Pyrus communis* H *Schinus areira* B	*Cotoneaster lacteus* B *Photinia serratifolia* B *Pinus radiata* W
Decreasers	*Ailanthus altissima* S *Cytisus scoparius* O *Gleditsia triacanthos* O *Ligustrum sinense* B *Lycium ferocissimum* B *Prunus persica* H *Syringa vulgaris* O *Ulex europaeus* O *Ulmus procera* S	*Cotoneaster glaucophyllus* B *Cotoneaster lucidus* B *Cotoneaster pannosus* B *Jasminum* sp. O *Ligustrum lucidum* B *Ligustrum sinense* B *Ligustrum vulgare* B *Lycium ferocissimum* B *Malus domestica* H *Prunus cerasifera* B *Prunus persica* H *Pyracantha crenulata* B

Others, perhaps with shorter life cycles (e.g. species of *Ligustrum* and *Pyracantha*), or a longer history of extensive planting (e.g. *Crataegus monogyna*, Bass 1996b), are at more advanced stages of invasion. They are already spreading rapidly in rural areas and some (e.g. *Ligustrum sinense*) may even be approaching the margins of those areas within their climatic tolerance.

Of greater novelty is the observation in both studies that wind-dispersed species are concentrated in the recent invader

category. *Acer negundo*, *Cupressus* sp. 995 and *Fraxinus angustifolia* appear as recent invaders in both studies, with *Pinus* other than *P. radiata* and *Ulmus parvifolia* appearing on single lists. The only wind-dispersed species in any other category, *Pinus radiata*, is an increaser in the roadside study and unchanged in the city study. This concentration of wind-dispersed species among the recent invaders appears to reflect the slower rate of invasion (or longer 'sleeper' period) of these plants compared with bird-dispersed ones. While bird-dispersed species have already spread widely, wind-dispersed ones equally capable of invasion of local habitats apparently have taken longer to spread, but are now in process of doing so. Indeed, it is possible that further wind-dispersed taxa are yet to begin their invasions. Only seven of the 63 species recorded in this overall study (11%) are wind-dispersed, while Binggeli (1996) noted that worldwide 40% of all woody invaders, and 28% of highly invasive species, are wind-dispersed.

Suckering species also appear to be invading, with (in the roadside study) seven of 10 species categorized either as increasers or recent invaders. However, it must be remembered that although suckering results in local thickets, it cannot disperse new plants to new places (at least without additional agents such as earth-moving equipment). While it may lead to locally significant environmental impacts, suckering without human intervention can result in only very gradual regional invasion.

It is generally not until after naturalization that the negative potential of particular woody plant invasions becomes fully apparent and arouses concern leading toward attempts at their control. However, only newly invading species are likely still to be at a stage where eradication remains possible (Weiss 1999), and lack of early treatment may quickly lead to a major problem (Hobbs and Humphries 1995). Such species, before their invasion potential becomes obvious, may be viewed positively by the general population and even regarded as regional icons (e.g. *Pistacia chinensis* in Armidale, Smith *et al*. in press). Fuller documentation of the early stages of plant invasion (Hobbs 1993) is needed for fuller and wider understanding of the potential for future invasions, leading towards more rational and effective action to avoid and manage them.

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