Mortality of a herbivorous insect is greater on non-indigenous congeneric compared to native rush in coastal salt marsh

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Abstract   Within endangered coastal salt marsh of south-east Australia, the non-indigenous rush *Juncus acutus* L. (Juncaceae) is displacing the native rush *Juncus kraussii* Hochst. (Juncaceae), with concurrent changes to the structure and composition of insect species assemblages. Here we test hypotheses that the abundance of a common and widespread sap-sucking herbivore, the planthopper *Haplodelphax iuncicola* Kirkaldy (Hemiptera: Delphacidae), differed between the non-indigenous *J. acutus* and the native *J. kraussii*, and that these differences were due to differential survivorship. Surveys at two salt marshes revealed that there were significantly fewer *H. iuncicola* on *J. acutus* than *J. kraussii*, and that *J. kraussii* at sites not invaded by *J. acutus* supported more than double the number of *H. iuncicola* than *J. kraussii* at invaded sites. A field experiment enclosing *H. iuncicola* on both *Juncus* species revealed complete mortality of planthoppers on the non-indigenous rush *J. acutus* in about 2 weeks, whereas there was greater than 80% survivorship on the native rush *J. kraussii*. Measurements of plant architecture showed that *J. acutus* is structurally different to the native rush *J. kraussii*, with thicker, taller and less densely packed stems, suggesting that *J. acutus* might therefore provide unsuitable habitat or food resources for *H. iuncicola*. These results suggest that *J. acutus* does not play a functionally similar role to *J. kraussii* for native insect assemblages.

Key words   Australia, invasive species, *Juncus acutus*, natural enemies hypothesis, plant architecture, planthopper.

INTRODUCTION

Invasion by non-indigenous plant species can alter native plant assemblages, leading to losses of specialist herbivores, changes to patterns of herbivory and alterations to insect community structure and ecosystem function (Walker & Smith 1997; Prieur-Richard & Lavorel 2000). The impacts of invasive plants can be detected by observation of associated insects, which are often sensitive to a variety of plant and habitat variables and can respond rapidly to change (Majer *et al*. 2002). Indeed, studies have demonstrated substantial differences in abundance and diversity of insect species between co-occurring native and non-indigenous plant species (French & Eardley 1997; French & Major 2001; Talley & Levin 2001; Herrera & Dudley 2003; Greenwood *et al*. 2004; Gratton & Denno 2005). By attracting fewer insects, non-indigenous plant invaders might confer resistance to herbivory on neighbouring native plant species (i.e. associational resistance) (Tahvanainen & Root 1972). Alternately, the presence of a non-indigenous plant in the landscape could mediate herbivore attack on the native plant community (i.e. associational susceptibility) (Rand 2003; Rand & Louda 2004; Lau &

Strauss 2005). A lack of natural enemies such as herbivorous insects may facilitate the rapid spread of non-indigenous plants into native communities (Colautti *et al*. 2004 and references therein; DeWalt *et al*. 2004; Vila *et al*. 2005; Blumenthal 2006; Liu & Stiling 2006; Proches *et al*. 2008).

Two principal explanations have been advanced to account for differences in the patterns of abundance and diversity of herbivorous insects between native and non-indigenous plants: nutritive value and plant architecture. Nutritive value, including chemical composition, water content, biomass, trichome density and mechanical properties, can vary greatly among species and has been shown to influence host plant selection, palatability and the demography and population dynamics of many insect taxa (Crawley 1983; Denno *et al*. 1986; Agrawal *et al*. 2005). Variations in plant architecture (*sensu* Lawton & Schroeder 1977), including differences in the size, growth form and types of aboveground and belowground structures of the host plant, can provide different microhabitats for insect herbivores and thus influence their colonisation and survivorship (Andersen 1987; Denno 1994a,b; Alonso & Herrera 2000). Differences in shape and structural complexity between non-indigenous and native plants can result in variations in light penetration (Flanagan 1997), suitability for resting, feeding, reproduction and nest building, and protection from abiotic stresses and predators (Strong *et al*. 1984; Denno

1994a). Gratton and Denno (2005), for example, found differences in the species composition of the insect fauna between salt marshes invaded by a non-indigenous genotype of the grass *Phragmites australis* compared to those dominated by the native grass *Spartina alterniflora*, and attributed these to differences in plant architecture (see also Hedge & Kriwoken 2000; Petillon *et al*. 2005). Nevertheless, few studies have examined experimentally in the field the demographic processes that might explain differences in the abundance of herbivorous insects between native and non-indigenous species.

In New South Wales (NSW), Australia, the non-indigenous rush *Juncus acutus* is rapidly invading the upper border of endangered coastal salt marshes, forming monocultures and displacing the native rush *Juncus kraussii* (Parsons & Cuthbertson 1992; Adam 2002; Pickthall *et al*. 2004; Zedler & Kercher 2004). Although there has been considerable speculation about the ecological consequences associated with the invasion of *J. acutus*, studies have largely focused on patterns of abundance, life history, and methods for control (Flanagan 1997; Greenwood & MacFarlane 2006; Kelleway *et al*. 2007). The only study that has examined the influence of *J. acutus* on associated herbivores has found dramatic differences in insect diversity and trophic structure between *J. acutus* and *J. kraussii* (Harvey *et al*. 2010). Moreover, Harvey (2006) observed that the most common and widespread, phloem-feeding planthopper *Haplodelphax iuncicola* appeared to be less abundant on the non-indigenous rush *J. acutus* compared to the native *J. kraussii* (Harvey *et al*. 2010). Invasion by *J. acutus* might be predicted to have strong negative effects on herbivorous insect species, such as delphacids, because they are generally monophagous on only a few species of host plants (Cook & Denno 1994). Nevertheless, closely related taxa, such as the congeneric rushes here, often share similar structural features, as well as compounds that determine their palatability for phytophagous insects (Tallamy 2004) and, consequently, native herbivores might be able to adapt to a close relative of the native plant species (Strong *et al*. 1984; Tallamy 2004).

Here we report the results of field surveys and a short-term experiment designed to test hypotheses that the abundance and survivorship of the planthopper *H. iuncicola* differs between the non-indigenous rush *J. acutus* and its native congener *J. kraussii*. We not only compared abundances of planthoppers between the congeneric rushes at sites invaded by *J. acutus*, but also between individuals of the native *J. kraussii* at sites either invaded or not invaded by *J. acutus*. The latter comparison was done to determine if the abundance of *H. iuncicola*, and therefore its potential for herbivory, on *J. kraussii* is mediated or resisted by being associated with neighbouring *J. acutus* in the landscape. We then experimentally enclosed *H. iuncicola* on each of the rush species and determined their survivorship over time. Differential survivorship may suggest that there are differences in suitability of each species as food or habitat for *H. iuncicola*. We also quantified differences in the architecture between *J. acutus* and *J. kraussii* to determine whether variations in plant structure might help to explain patterns of abundance and survivorship of *H. iuncicola*.

MATERIALS AND METHODS

Locations and species studied

The study was conducted in two coastal, intertidal locations comprising mangrove forests and salt marshes within the urbanised landscape of Sydney, NSW, Australia: Towra Point Nature Reserve (34°1′19.42″S 151°11′40.81″E) and Salt Pan Creek 33°57′46.56″S 151°1′19.25″E). Towra Point Nature Reserve (hereafter Towra Point) is located at the mouth of the Georges River in Botany Bay, and Salt Pan Creek is a tributary of the Georges River, 16 km inland of and within the same estuary as Towra Point. The salt marshes have mangroves (primarily *Avicennia marina* (Forssk.) Vierh., but also *Aegiceras corniculatum* (L.) Blanco) along their seaward edges and plant communities dominated by the tree *Casuarina glauca* Sieber ex Spreng. along their landward borders. Salt marshes at both locations are comprised of plant species characteristic of salt marshes in NSW (Adam 1981; Adam *et al*. 1988; Pickthall *et al*. 2004). The plant communities in the marshes are dominated by the native rush *J. kraussii* along the upper border of the marsh adjacent to *C. glauca* and the terrestrial landscape, and the chenopods *Sarcocornia quinqueflora* (Bunge ex Ungen-Sternberg) A.J. Scott and *Suaeda australis* (R. Brown) Moquin-Tandon and the grass *Sporobolus virginicus* (L.) Kunth at the lower tidal elevations between *Juncus* spp. and the mangroves.

At Towra Point and Salt Pan Creek, and throughout southeast Australia, the non-indigenous rush *J. acutus* (commonly referred to as spiny rush) has invaded the terrestrial salt marsh ecotone and seaward into the higher tidal elevations of the salt marsh characteristically dominated by the native rush *J. kraussii* (Robinson 1991; Adam 2002; Pickthall *et al*. 2004). *J. acutus* is a declared noxious weed in the state of Victoria, Australia, and its invasion is of particular concern in NSW where Coastal Saltmarsh is listed as an Endangered Ecological Community under the NSW Threatened Species Conservation Act (Department of Environment, Climate Change and Water 2008). In NSW, *J. acutus* is now commonly found interspersed among *J. kraussii* along the terrestrial border, particularly in urban landscapes, fragmenting the upper marsh habitat normally dominated by *J. kraussii*, and displacing this species and other native salt marsh vegetation (Parsons & Cuthbertson 1992; Adam 2002; Zedler & Kercher 2004; Greenwood & MacFarlane 2006). In Australia, *J. acutus* can grow to up to 2 m in height, often forming dense, monospecific stands (Parsons & Cuthbertson 1992). *J. acutus* is apparently more robust than many of the native rushes on the south-east coast of Australia, with larger tussocks and thicker and tougher stems (Parsons & Cuthbertson 1992; Snogerup 1993; Laegdsgaard 2006).

Haplodelphax iuncicola is a small (approximately 3 mm total body length), phloem-feeding insect found throughout eastern Australia and belongs to the more advanced tribe of Delphacini (Fennah 1965; Wilson *et al*. 1994). Delphacids are intimately associated with their host plants, using them for feeding, mating, oviposition and protection from climate and

their natural enemies (Wilson *et al.* 1994). The cosmopolitan Delphacidae are relatively host plant specific and typically feed from the phloem of one or a few plant species within the same genus of monocots, including Poaceae, Cyperaceae and Juncaceae (Wilson *et al.* 1994). Consequently, delphacids might be expected to colonise and live on closely related species of *Juncus*. The nymphs and adults of delphacids occur together on the aboveground parts of their host plants, although most species inhabit the basal portion or tussock of the plant and are associated with the basal meristem (Cook & Denno 1994). Local populations of *H. iuncicola* often include both macropters and flightless brachypters, a situation common in some species of delphacids (G. Bellis pers. comm. 2006). Only brachypterous individuals were found in this study.

Abundance of *Haplodelphax iuncicola*

The abundance of *H. iuncicola* on *J. acutus* and *J. kraussii* was estimated at two sites in upper salt marsh dominated by *Juncus* spp. at each study location (Towra Point and Salt Pan Creek). One site was dominated by the native rush *J. kraussii* and invaded by the non-indigenous rush *J. acutus* (allowing comparisons between congeneric rushes at the one site), and the other was dominated by *J. kraussii* and not invaded by *J. acutus* (allowing comparisons of *J. kraussii* between locations either invaded or not invaded by *J. acutus*). Sites at each location extended 80 m alongshore and 40 m seaward from the terrestrial border of the marsh and were separated by about 2 km. At invaded sites, *J. acutus* occupied about 30% of the cover of vegetation and was interspersed throughout the area dominated by *J. kraussii* (which occupied a minimum of 40% and a maximum of 73% cover). At both locations, sites not invaded by *J. acutus* had approximately 95% cover of *J. kraussii*.

Haplodelphax iuncicola were sampled during low tide, between 10:00 and 14:00 h, from 8 to 11 February 2006 at Towra Point and Salt Pan Creek. A different site was sampled on each day, and temperatures ranged 25–32°C with full sunshine. At each site, insect assemblages were sampled in each of six, randomly selected quadrats (1 m × 1 m, and separated by at least 2 m) for *J. acutus* and *J. kraussii* at invaded sites and for *J. kraussii* only at non-invaded sites. The quadrat size was based on the average area of a single, large plant of *J. acutus* at these locations. For *J. acutus*, quadrats were centred on single plants of roughly this size, and for *J. kraussii* quadrats often included several individual plants. The equivalent area of 1 m² was sampled for *J. kraussii* because this is the same ground area occupied by a single plant of *J. acutus*. The assumption made was that this provided equivalent potential habitat for insect herbivores.

Sampling was done using three techniques: sweep netting of the stems of plants, vacuum sampling of the tussock of plants and vacuum sampling of the ground directly beneath the plants. Sampling methods were based on those of Gratton and Denno (2005), and pilot studies were done to determine the required duration of vacuum sampling and number of samples

that was needed to exhaustively collect insects present on the plants within a quadrat. The latter was assessed by constructing species accumulation curves for *J. acutus* and *J. kraussii* (K. Harvey unpubl. data 2006).

Sweep netting was performed first to sample insects resting externally on the stems above the tussock of plants. Ten sweeps were made within the 1 m² quadrat using a sweep net with an opening diameter of 37 cm and an effective volume of 0.12 m³. After sweep netting, the tussock of the single *J. acutus* plant, or the equivalent 1 m² area of *J. kraussii*, was vacuumed for 30 s using a two stroke petrol garden vacuum (RYOBI RGBV3100) fitted with a sampling head with a diameter of 11 cm and a bag volume of 0.04 m³. Finally, a 10 s vacuum sample from the ground was taken within two strips (50 cm × 20 cm) totalling an area of 0.055 m². The two strips were positioned on either side of the tussock for *J. acutus*, and in an equivalent area within the 1 m² quadrat for *J. kraussii*. All three samples were combined to yield an estimate of insect abundance per quadrat.

Survivorship of *Haplodelphax iuncicola*

The survivorship of *H. iuncicola* on the native rush *J. kraussii* was compared to that on the invasive rush *J. acutus* at a site invaded by *J. acutus* at Towra Point in May 2006. Over 400 individuals of *H. iuncicola* (brachypterous) were collected using a vacuum from the tussock of pure stands of *J. kraussii* in an area of salt marsh (80 m × 40 m) not invaded by *J. acutus* and located in the same stands as per summer sampling, about 1.5 km from the invaded site at Towra Point. Individuals were only collected from the native *J. kraussii* because this would represent the natural situation where *J. acutus* might invade an area providing individuals of *H. iuncicola* with an opportunity to move onto *J. acutus*. Samples were cooled in a refrigerator for 12 h before sorting and transferring to the field.

Forty white opaque sleeve enclosures made from polyester organza fabric (30 cm × 15 cm; mesh size: 0.3 mm × 0.3 mm) were attached to live stems of 20 randomly selected *J. acutus* and 20 *J. kraussii* plants. Each sleeve enclosed a stem length of approximately 20 cm and contained one stem of *J. acutus* or two stems of *J. kraussii* which is an approximate equivalent stem volume of *J. acutus.* Sleeves were slid over the stems, positioned at the tussock region (i.e. basal portion) of the plant and closed at each end using metal twist ties. Ten *H. iuncicola* adults from field samples were randomly selected regardless of their sex and placed in each sleeve and survival rates monitored.

Pilot studies indicated that assessing survivorship in the field was not possible because it was difficult to determine whether individuals were alive within the enclosures. The study was designed so that replicate sleeves could be removed from the field and percentage survivorship assessed in the laboratory after 2, 4, 8, 12 and 16 days in the field, after which the experiment was terminated. Two replicates were initially collected within the first few days of the experiment and more replicates were collected when differences in survivorship were apparent. Three replicates of *J. acutus* and three repli-

cates of *J. kraussii* were lost and not included in analyses. No tides reached the treatment sites during the sampling period.

Differences in plant architecture

Differences in plant architecture between *J. acutus* and *J. kraussii* were quantified by measuring stem density, stem thickness, stem height and the distance between stems within the tussock and at the mid height of plants. The sampling design was identical to that described above for assessing abundance of *H. iuncicola*, except that five subquadrats (10 cm × 10 cm) were sampled within each of five (not six) 1 m² quadrats for all variables except stem height. For each of the variables measured in the five subquadrats, the mean value from these measures gave a single estimate of the variable per quadrat. Within each subquadrat, stem density was estimated as the total number of stems, stem thickness as the mean of five stems (using Vernier calipers) at the mid height of the plant and distance between stems as the mean of five stems within

the tussock and at mid height of the plant. Stem height was estimated as the mean height of five stems per 1 m² quadrat.

Statistical analyses

Two comparisons examined the difference in the density of *H. iuncicola* and plant architecture (stem density, stem thickness, stem height and distance between stems at mid and tussock height): (1) the non-indigenous rush *J. acutus* was compared to the native rush *J. kraussii* at sites invaded by *J. acutus* for each of the two locations (Towra Point, Salt Pan Creek) (see Table 1); (2) the native rush *J. kraussii* was compared between sites either invaded or not invaded by *J. acutus* at each of the two locations (Towra Point, Salt Pan Creek) (see Table 2). For the first comparison, two-factor (plant species, location) mixed model analysis of variance (ANOVA) was used, and plant species (*J. kraussii* or *J. acutus*) was considered a fixed factor and location (Towra Point or Salt Pan Creek) a random factor. For the second, two-factor, nested ANOVA (invasion, sites

Table 1 Results of two-factor, analysis of variance for the effect of plant species (*Juncus acutus* or *Juncus kraussii*; d.f. = 1, 1), location (Towra Point or Salt Pan Creek; d.f. = 1, 20 for abundance of *Haplodelphax iuncicola*; d.f. = 1, 16 for architecture: stem density, stem thickness, stem height and distance between stems at mid and tussock height) and their interaction (d.f. = 1, 20 (abundance *H. iuncicola*), d.f. = 1,16 (architecture)) on the abundance of *H. iuncicola* and differences in plant architecture. For all variables, data were transformed to log (x + 1)

Variable	Plant species		Location		Species × location		Residual
	MS	P	MS	P	MS	P	MS
Haplodelphax iuncicola							
Abundance	1.132†	0.044	1.628	0.020	0.069	0.609	0.256
Architecture							
Stem density	0.122	0.001	0.549	0.326	<0.001	0.998	0.053
Stem height	0.060†	0.031	0.001	0.735	0.011	0.324	0.011
Stem thickness	0.155†	<0.001	0.003	0.371	0.002	0.407	0.003
Distance between stems: mid height	0.231†	0.007	0.118	0.034	0.069	0.095	0.022
Distance between stems: tussock height	0.205†	0.030	0.083	0.162	0.010	0.625	0.038

†To increase the power of the test, the estimate of MS used in the denominator of the *F*-ratio is a pooled estimate from the MS of the Species × Location interaction and the residual (see Winer *et al*. 1991 for pooling procedures).

Table 2 Results of two-factor, nested analysis of variance for the effect of invasion (presence or absence of *Juncus acutus* at a site; d.f. = 1, 2) and sites nested within invasion at each location (Towra Point or Salt Pan Creek; d.f. = 2, 20 for abundance *Haplodelphax iuncicola*; d.f. = 2, 16 for architecture: stem density, stem thickness, stem height and distance between stems at mid and tussock height) on the abundance of *H. iuncicola* and differences in plant architecture. With the exception of the abundance of *H. iuncicola* all variables were transformed to log (x + 1)

Variable	Invasion		Site (Invasion)		Residual
	MS	P	MS	P	MS
Haplodelphax iuncicola					
Abundance	4959.380	0.017	85.208	0.881	667.558
Architecture					
Stem density	0.165	0.154	0.033	0.056	0.054
Stem height	0.003	0.811	0.035	0.010	0.006
Stem thickness	<0.001	0.731	0.004	0.038	<0.001
Distance between stems: mid height	0.009	0.792	0.102	0.018	0.019
Distance between stems: tussock height	0.176†	0.038	0.039	0.347	0.035

†To increase the power of the test, the estimate of MS used in the denominator of the *F*-ratio is a pooled estimate from the MS of Site (Invasion) and the residual (see Winer *et al*. 1991 for pooling procedures).

nested within invasion) was used, and invasion (presence or absence of *J. acutus* at a site) was considered a fixed factor and sites nested within invasion at each location (Towra Point or Salt Pan Creek) a random factor. Where appropriate, data were log-transformed before analysis to homogenise variances. Where there was low power to detect differences in the main factor of interest (i.e. differences between plant species or between *J. kraussii* at sites either invaded or not invaded by *J. acutus*) due to great variability among sites, post-hoc pooling of terms in the ANOVA was performed according to the procedures of Winer *et al.* (1991). Differences in percentage survivorship of *H. iuncicola* between *J. acutus* and *J. kraussii* were tested using independent *t*-tests for each sampling time: day 2, 4, 8 and 16.

RESULTS

There were striking differences in the mean abundance of the planthopper *H. iuncicola* between native and non-indigenous rushes, as well as between sites either invaded or not invaded by *J. acutus*. The number of *H. iuncicola* on the non-indigenous rush *J. acutus* was significantly smaller than on the native rush *J. kraussii* (Fig. 1a, Table 1). In addition, the abundance of *H. iuncicola* on *J. kraussii* at sites not invaded by *J. acutus* was more than double and significantly greater than that on *J. kraussii* at invaded sites, suggesting an effect of invasion on overall planthopper numbers in a marsh (Fig. 1a, Table 2).

There were dramatic differences in the survivorship of *H. iuncicola* between the non-indigenous and native rush species. After only 4 days, about 30% of *H. iuncicola* on *J. acutus* were dead, although there were no significant differences in survivorship at this time (Fig. 1b, $t = 1.96$; d.f. = 2; $P = 0.190$). Survivorship of *H. iuncicola* declined rapidly on *J. acutus* after 4 days, and mortality of planthoppers on *J. acutus* was significantly greater than on *J. kraussii* after 8 ($t = 13.53$; d.f. = 10; $P < 0.001$), 12 ($t = 7.89$; d.f. = 2; $P = 0.016$) and 16 days ($t = 4.93$; d.f. = 8; $P = 0.001$). After 16 days, all individuals on *J. acutus* were dead, whereas survivorship of *H. iuncicola* on *J. kraussii* declined less than 20% throughout the entire 16 day period (Fig. 1b).

The structural architecture of the non-indigenous rush *J. acutus* was substantially different to that of the native rush *J. kraussii* in ways that might be expected to influence the movement and feeding of planthopper *H. iuncicola* (Fig. 2). *Juncus acutus* had a significantly sparser density of stems and these were more widely spaced at both the mid height and within the tussock of the plant (Fig. 2, Table 1). Moreover, individual stems of *J. acutus* were significantly taller than and twice as thick as those of *J. kraussii* (Fig. 2, Table 1). Not surprisingly, there were no substantial differences in plant architecture for *J. kraussii* at sites either invaded or not invaded by *J. acutus*, with the exception of distance between stems in the tussock, which was significantly greater for plants at invaded sites (Fig. 2, Table 2).

DISCUSSION

In areas of salt marsh invaded by *J. acutus*, the native rush *J. kraussii* supported about twice the numbers of *H. iuncicola* than the non-indigenous rush *J. acutus*, suggesting that native rushes provide more suitable habitat than the closely related non-indigenous congener. There was complete mortality of *H. iuncicola* enclosed on the non-indigenous rush *J. acutus*, which might account for reduced numbers of planthoppers on *J. acutus*. Notably, the abundance of *H. iuncicola* on *J. kraussi* was also dependent on whether sites had been invaded by *J. acutus*, with native rushes at non-invaded sites having more than double the number of planthoppers than at invaded sites. This result suggests that even the presence of *J. acutus* in the salt marsh landscape might have a detrimental influence on planthoppers on the native *J. kraussii*.

Our results support findings of other studies that insect abundance on non-indigenous plants can be reduced compared to native species (French & Eardley 1997, French & Major 2001; Greenwood *et al.* 2004; Gratton & Denno 2005). Determining the life history process that might limit insect abundance on non-indigenous species is a crucial first step in determining how such novel species might influence native insect abundance. Our field experiments demonstrate that survival of brachypterous individuals is severely reduced on non-indigenous rushes, and this might account for observed differences in abundance compared to congeneric natives. Field studies manipulating insects and examining their subsequent demography are few, but other studies have reported that non-indigenous species can reduce the performance and survivorship of larval insects compared to native plants (Straatman 1962; DiTommaso & Losey 2003; Tallamy *et al.* 2010). The final step would be to determine mechanisms that might influence insect survival on non-indigenous compared to native congeneric rushes.

Differences in the structural, chemical or nutritional properties of *J. acutus* might make it unsuitable as a host plant for *H. iuncicola* and thus account for the reduced abundance and increased mortality on non-indigenous compared to native rushes, although this study was not designed to ascertain or distinguish these mechanisms. Other studies have demonstrated that survivorship of herbivorous insects may be influenced by host plant nutrition or chemistry (CSIRO 1991; Braby 2000; Renwick *et al.* 2001; Stastny *et al.* 2005), and this may be particularly important for planthoppers, which are often host plant specific (Crawley 1983; Denno & Roderick 1990; Cook & Denno 1994). The chemical composition of *J. acutus* and the potential effects on insects is unknown, but *J. acutus* is known to contain a secondary plant chemical that inhibits the growth of green algae (Dellagreca *et al.* 2004). Failure of this planthopper to survive on a specific host plant may also result from the presence of feeding inhibitors or toxins, the absence of feeding stimulants (Cook & Denno 1994), inadequate plant nitrogen (Crawley 1983; Denno & Roderick 1990; Cook & Denno 1994) or its inability to locate or reach the phloem. *J. acutus* has thicker stems than *J. kraussii* or may have cuticular wax that could create a barrier
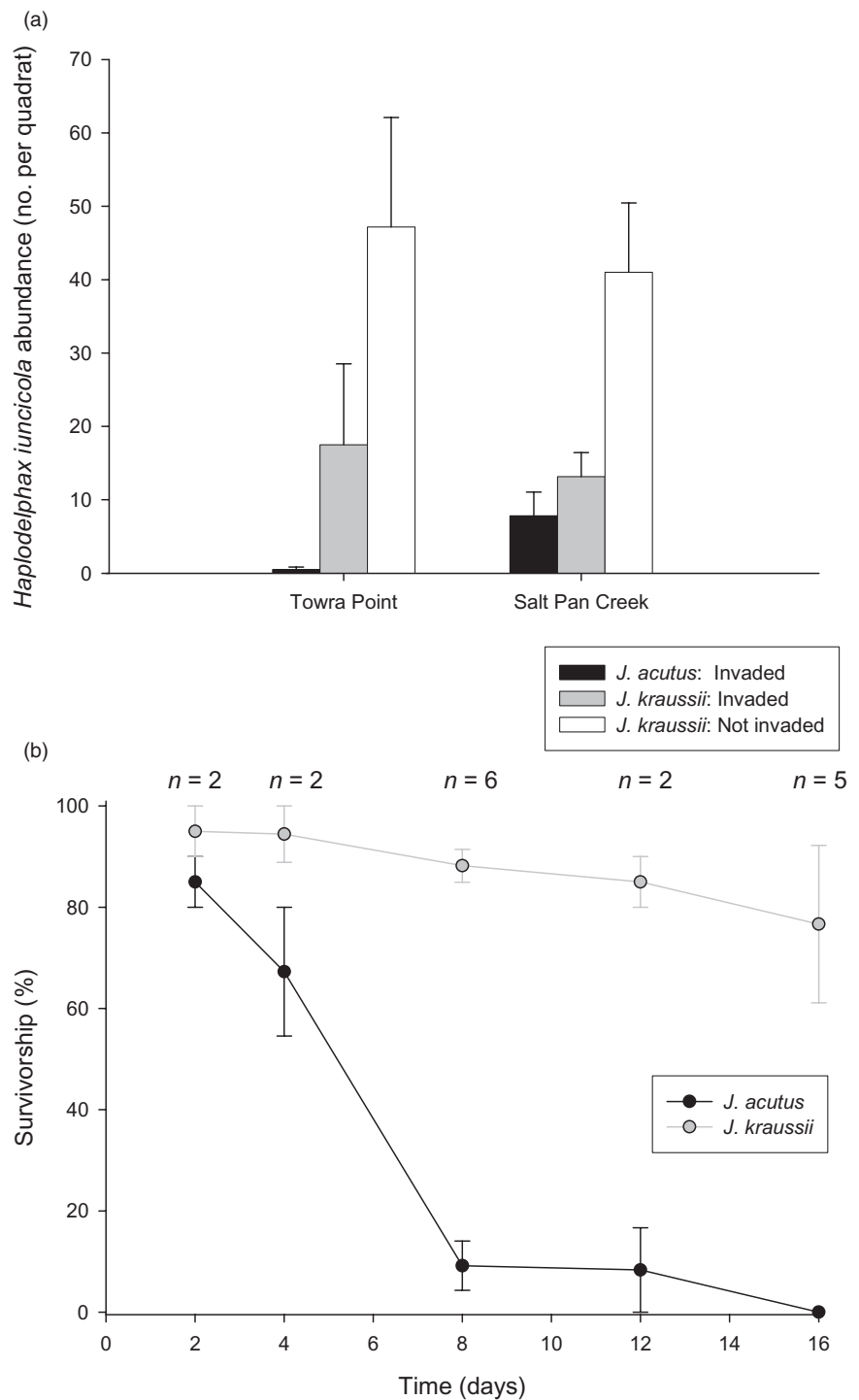
(a)

(b)

Fig. 1. (a) Mean (±SE) abundance of *Haplodelphax iuncicola* on the invasive rush *Juncus acutus* and the native rush *Juncus kraussii* at sites invaded by *J. acutus* and on *J. kraussii* at sites not invaded by *J. acutus* at Towra Point and Salt Pan Creek, and (b) percentage survivorship (±SE) of *H. iuncicola* on the invasive rush *J. acutus* and the native rush *J. kraussii* over 16 days. *n*, number of sleeves removed at each sampling time.

(e.g. see Woodhead and Padgham 1988 for planthopper feeding on rice cultivars). The planthopper *Nilparvata lugens* is able to locate and feed on the phloem of the grass *Oryza sativa* with its stylets, but is unable to do so on the closely related grass *Leersia hexandra*, suggesting the involvement of a specific feeding stimulant (Cook & Denno 1994). Thus, *J. acutus* may not be providing suitable feeding stimulants for this insect species, such as an appropriate concentration of sucrose that would promote the injection of the feeding stylet (Sakai & Sogawa 1976).

The reduced abundance of *H. iuncicola* on non-indigenous *J. acutus* might also be due to the effects of plant architecture on mate location and fecundity, which may indirectly influence the survivorship of *H. iuncicola*. Mate location in brachypterous planthoppers is often at least partially dependent on acoustic signals transmitted through the plant (Claridge 1985; Denno & Roderick 1990). Moreover, plant stems need to be touching in order for brachypterous individuals to locate mates (Ichikawa *et al*. 1974; Ichikawa 1976). Thus, the greater distances between and smaller densities of stems for *J. acutus*
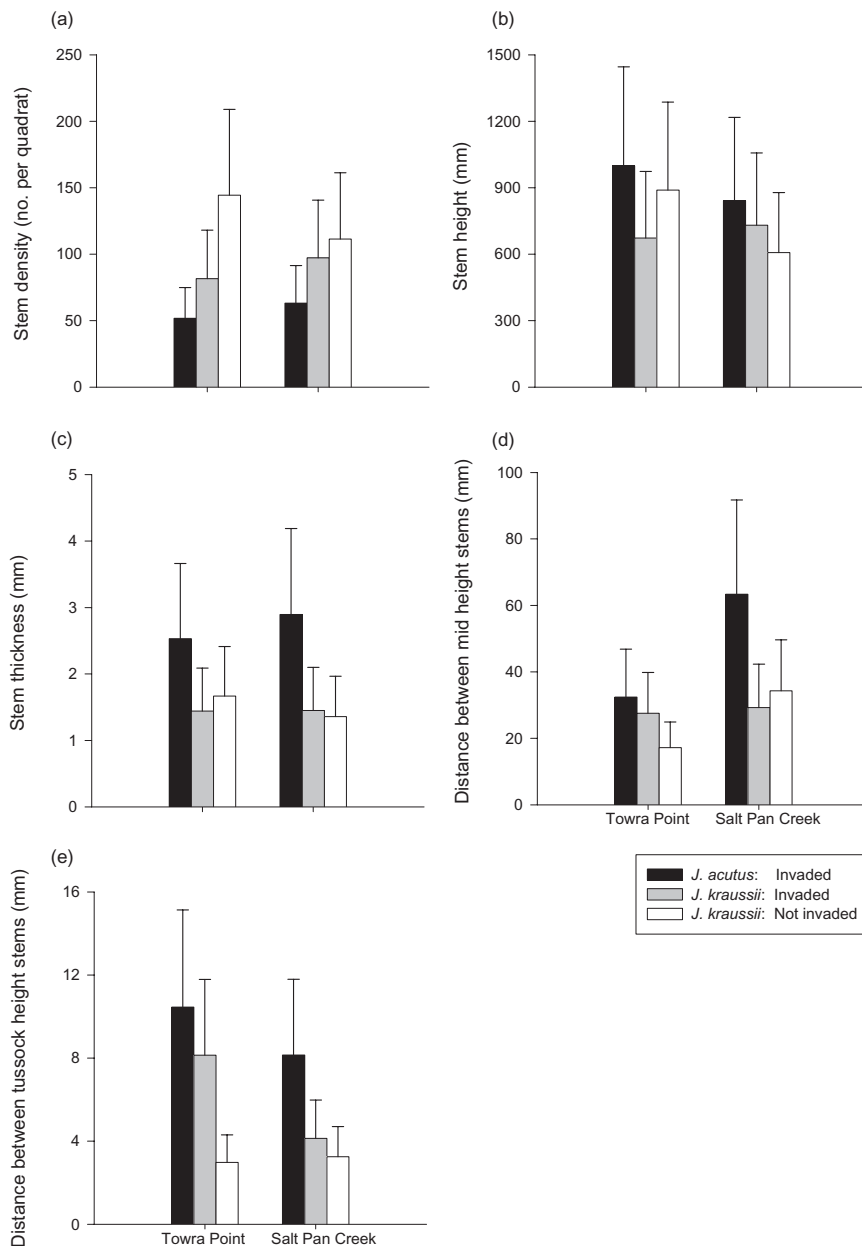
Fig. 2. Mean (±SE) (a) density of stems, (b) height of stems, (c) thickness of stems and distance between the stems at (d) mid height and (e) tussock of the plant for the invasive rush *Juncus acutus* and the native rush *Juncus kraussii* at sites invaded by *J. acutus* and on *J. kraussii* at sites not invaded by *J. acutus* at Towra Point and Salt Pan Creek.

compared to the native *J. kraussii* might influence mate location and thus deter *H. iuncicola* from colonising *J. acutus*. The presence of an invasive plant in the landscape may interfere with mate location and oviposition in planthoppers (R. Denno pers. comm. 2006). In addition, stem thickness has been shown to be negatively correlated with fecundity in the planthopper *Javesella pellucida* (Raatikainen 1967). This suggests that the thicker stems of *J. acutus* may reduce the number of eggs that *H. iuncicola* deposits into the stems and thus overall fecundity. Nevertheless, the degree to which plant structures, such as the thickness, density or texture of stems can directly interfere with acoustic signals and ultimately reproduction in planthoppers is largely unknown and warrants further investigation (R. Denno pers. comm. 2006).

The greater abundance of *H. iuncicola* on *J. kraussii* in salt marsh dominated by pure stands of this native rush com-

pared to areas invaded by *J. acutus* suggests that there are landscape-scale effects of invasion. It appears that the mere presence of *J. acutus* in the landscape might be influencing the abundance of *H. iuncicola* in a marsh. Invasion by *J. acutus* fragments the continuous habitat provided by stands of native *J. kraussii* and may influence the movement of individuals, particularly for brachypterous *H. iuncicola* which may be unable to move more than a few metres in a lifespan (Raatikainen 1967; Denno *et al*. 1980). Thus, *H. iuncicola* may have limited ability to escape and colonise more favourable habitats. Fragmentation of a community, differences in plant architecture and the presence of invasive plants have been demonstrated to influence the densities of herbivorous insects and predators on their hosts by changing the microhabitats suitable for protection, habitat and shading (Denno 1994a), altering movement, searching efficiency and

colonisation, or by interfering chemically with host finding behaviour (Kareiva 1987; Denno 1994a). For example, the more open tussocks of *J. acutus* compared to *J. kraussii* might alter the microclimate, reducing humidity and increasing insolation, which for planthoppers may result in desiccation or overheating.

The results of this study indicate that invasion of *J. acutus* may have a direct influence on the abundance and survivorship of *H. iuncicola* in coastal salt marsh. Further generalisations based on results of this experiment are limited at this stage. The experiment was done at one time of the year, and plant food resources can vary temporally (Strong *et al*. 1984) and many invertebrates are known to synchronise their life cycles in response to nutrient availability in the plant (Cook & Denno 1994). If *J. acutus* provides unsuitable habitat for or is toxic to herbivorous insects such as *H. iuncicola*, then this consequent release from natural enemies might account for its success as an invader (Harvey *et al*. 2010). Regardless, this study suggests that the replacement of *J. kraussii* with *J. acutus* could potentially result in the depletion or local extinction of *H. iuncicola* in these systems, and this may influence a variety of other native insects.

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