

Great house, poor food: effects of exotic leaf litter on shredder densities and caddisfly growth in 6 subtropical Australian streams

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Abstract. Exotic plants have invaded the riparian zones of many streams worldwide, but their consequences for stream fauna are seldom fully appreciated, especially when effects are sublethal. In northern New South Wales, Australia, the exotic tree camphor laurel (*Cinnamomum camphora*) has aggressively invaded riparian zones of many subtropical streams, often forming monocultures and outcompeting native vegetation. In forested streams, leaf litter provides a major source of food for some stream fauna and is broken down by shredding invertebrates. We hypothesized that shredder densities would be reduced in streams where the riparian zone was dominated by camphor laurel because of the reputed chemical toxicity of the leaf litter. We also investigated the sublethal effects of camphor laurel litter by comparing growth rates of larvae of the common shredding caddisfly *Anisocentropus* (Calamoceratidae: Trichoptera) reared on a diet of camphor laurel vs native leaf litter. Shredder densities were significantly lower in streams where camphor laurel constituted >38% of the benthic leaf litter than in streams with a lower percentage of camphor laurel litter (0.43 ± 0.13 vs 1.43 ± 0.28 individuals/g dry mass of litter; mean \pm SE). Shredder densities were greater on artificial packs of native leaf litter than on packs of camphor laurel litter in camphor laurel-infested streams (3.37 ± 1.01 vs 1.40 ± 0.46 ind./g dry mass of litter). However, shredder densities did not differ between leaf-litter types in streams lined with native vegetation. *Anisocentropus* growth was retarded when larvae were fed only camphor laurel compared to those reared on native leaf litter. This native caddisfly used camphor laurel leaves for case construction, but impaired larval growth in infested streams implies a sublethal impact that has repercussions for energy transfer to higher trophic levels (e.g., predatory fish). Our findings suggest effects similar to those often reported for shredder assemblages in temperate streams subject to invasion by exotic riparian plants, indicating that the tropical-temperate differences in this aspect of leaf breakdown might not be as marked as previously suspected. Carefully managed river restoration to remove camphor laurel to allow recovery by native vegetation is recommended in these streams. Population dynamics of *Anisocentropus* could provide a useful indicator of the ecological success of such restoration.

Key words: subtropical streams, exotic species, shredders, riparian-zone management, *Eucalyptus*, *Anisocentropus*, sublethal effects, leaf packs, river restoration.

Riparian leaf litter is a major source of energy for aquatic detritivores in forested streams (Fisher and Likens 1973, Wallace et al. 1997). In these streams, invertebrates capable of feeding directly on coarse particulate organic matter (shredders; Cummins and Klug 1979) play a fundamental role in organic matter breakdown and energy transfer (Petersen and Cummins 1974, Webster and Benfield 1986, Graça 2001). Shredders are rare in some tropical streams (reviewed in Wantzen and Wagner 2006), but they are common in many Australian tropical streams (Cheshire et al. 2005). One of the most abundant shredders in these streams is the calamoceratid caddisfly *Anisocentropus*

(Pearson and Tobin 1989, Boyero and Pearson 2006, Bastian et al. 2007), which uses leaves for food and case construction.

Leaf quality largely determines feeding behavior of shredders (Graça 2001) and, hence, their efficiency in converting leaf organic matter to secondary production. In Australian tropical streams, *Anisocentropus* discriminates among leaf species (Nolen and Pearson 1993, Clapcott and Bunn 2003) and competes with other shredders (leptocerid caddisflies and leptophlebiid mayflies) for preferred food sources (Boyero and Pearson 2006). This preference of shredders for particular leaf-litter species is relevant when considering the likely effects of changes in riparian-zone vegetation composition as a result of invasion by

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TABLE 1. Percent cover of *Cinnamomum camphora* (camphor laurel) and other dominant species of riparian-zone vegetation and ranges of physicochemical characteristics of 6 Orara Valley streams. Water-chemistry data were collected during August–September 2003 (*n* = 6). Temperature data are ranges from data loggers (Hobo; Onset Corporation, Bourne, Massachusetts), conductivity and pH were measured with a field-meter (TPS; Enviroquip, Brisbane, Australia), and nutrient concentrations were determined by standard methods (APHA 1992).

Characteristic	Coldwater Creek	Karangi Creek	Wongiwomble Creek	Dingo Creek	Poperaperan Creek	Wayper Creek
Location (lat, long)	30°6'19.80"S 153°0'18.00"E	30°15'18.00"S 153°3'28.80"E	30°15'54.00"S 153°2'45.60"E	30°18'43.20"S 152°58'55.20"E	30°14'06.00"S 153°3'00.00"E	30°15'46.80"S 152°59'54.00"E
Riparian-zone vegetation						
Camphor laurel	70%	85%	90%	0%	0%	0%
Native	30% <i>Eucalyptus</i> spp.	12% <i>Eucalyptus</i> spp., 3% <i>Callicoma serratifolia</i>	5% <i>Eucalyptus</i> spp.	95% (<i>Ficus coronata</i> , <i>C. serratifolia</i> , <i>Eucalyptus</i> spp., <i>Ceratopetalum apetalum</i>)	95% (<i>F. coronata</i> , <i>C. serratifolia</i> , <i>C. apetalum</i> , <i>Archontophoenix cunninghamiana</i>)	95% (<i>F. coronata</i> , <i>C. serratifolia</i> , <i>Eucalyptus</i> spp., <i>Tristaniopsis laurina</i> , <i>Platyserium superbum</i>)
Other exotic			5% <i>Ligustrum sinense</i>	5% <i>Lantana camara</i>	5% <i>L. camara</i>	5% <i>L. camara</i>
Channel width (m)	2.5–8.4	1.8–6.8	1.2–7.5	1.5–4.1	2.3–6.0	1.0–5.5
Median flow velocity (m/s)	0.11	0.15	0.34	0.20	0.35	0.27
Substratum	Cobble/pebble	Cobble/pebble	Cobble/pebble/sand	Cobble/pebble	Cobble/pebble/gravel	Boulder/cobble/pebble
Conductivity (µS/cm)	245–255	100–120	110–120	45–50	95–100	50–55
pH	7.15–7.66	7.30–7.63	7.36–7.42	6.94–7.37	7.63–8.07	6.90–7.43
Total N (mg/L)	0.10–0.20	0.17–0.25	0.20–0.25	0.07–0.19	0.76–1.12	0.01–0.04
Total P (mg/L)	<0.01	<0.01–0.03	<0.01–0.02	<0.01	0.07–0.09	<0.01
Water temperature (°C)	11.6–15.0	10.8–14.9	11.4–13.6	11.6–13.9	10.6–13.8	13.0–13.4

aggressive exotic plants, especially if the leaf litter is toxic or poor in quality (Smock and MacGregor 1988, Canhoto and Graça 1999). Since the early 1900s, the riparian zones of many subtropical streams in northern New South Wales (NSW), Australia, have become dominated by the exotic tree camphor laurel (*Cinnamomum camphora*), the leaf litter and roots of which contain allelochemicals (terpenes) capable of restricting growth of native species in the understory (Firth 1979). The leaf litter is also rich in secondary compounds and aromatic oils (Stubbs and Brushett 2001) that potentially can restrict microbial colonization known to enhance the palatability of leaf litter to many aquatic shredders (Webster and Benfield 1986).

The effect on the aquatic food webs in these subtropical streams of this replacement of native riparian vegetation with camphor laurel is poorly understood. Anecdotal evidence suggests that during periods of low flow, high concentrations of leachates from camphor laurel leaf litter reduce dissolved O₂, killing native fish and aquatic invertebrates (Llewellyn 2005). As a result, local government councils are commencing programs to poison and remove camphor laurel from accessible river banks. However, such programs run the risk of accelerating bank erosion or allowing other exotic weeds to become established. To assess the potential impacts of camphor laurel leaf litter on native shredders in these streams, we tested the following hypotheses: 1) lower densities of shredders occur in streams containing camphor laurel leaf litter, 2) densities of shredders are lower on artificial packs of camphor laurel litter than on packs of native leaf litter in streams without camphor laurel in the riparian zone, 3) densities of shredders, while low overall, are higher on artificial packs of native litter than on packs of camphor laurel in streams with riparian zones dominated by camphor laurel, and 4) growth of the shredding caddisfly *Anisocentropus* is retarded when reared on a diet of camphor laurel relative to growth on a diet of native eucalypt litter. Outcomes of these hypotheses would indicate whether camphor laurel removal is warranted and whether densities or growth of *Anisocentropus* might be a useful indicator of the ecological success of this river restoration strategy.

Study Area

The 6 study streams (Table 1) are tributaries of the upper Orara River, which flows into the Clarence River, the largest coastal drainage in northern New South Wales. The climate is warm-subtropical, and the region receives 1500 mm of rainfall annually, mostly in summer. The valley's geology is sedimentary mud-

stone (siliceous argillite) and graywacke sandstone, and the alluvial soils are primarily basaltic (Milford 1996). In the drier areas of the catchment, the vegetation is eucalypt-dominated sclerophyll forest (*Eucalyptus microcorys*, *Eucalyptus pilularis*), whereas wetter regions support remnant patches of rain forest dominated by sandpaper fig (*Ficus coronata*), water gum (*Tristaniopsis laurina*), and river box (*Callicoma serratifolia*) (Williams et al. 1984). *Callicoma serratifolia* also lines most of the creeks where camphor laurel is rare or absent, and it was used as the native leaf-litter treatment in the comparisons of stream fauna colonizing artificial leaf packs (see Riparian vegetation, benthic leaf-litter composition, and shredder densities section). The exotic tree camphor laurel was introduced into the Orara Valley in 1901 as a shade tree, and by the 1930s, it was well-established along the banks of the Orara River (R. Smith, Karangi, NSW, personal communication). Since then, camphor laurel has come to dominate the riparian zone of many of the tributaries of the Orara River, leaving only small patches of remnant eucalypts or river box. Streams completely free of camphor laurel are now uncommon in the valley.

Six 2nd-order streams sharing similar substrata, stream widths, and median current velocities (Table 1) were selected to yield 3 streams with camphor laurel dominating (70–90% cover) the riparian zone (infested streams) and 3 lacking camphor laurel (uninfested streams; Table 1). The streams varied slightly in water quality but were typically circumneutral in pH. Dissolved nutrient concentrations were low, except in Poperaperan Creek, where total N concentrations were relatively high (Table 1). At the time of the artificial leaf pack study when these comparative site data were collected (austral spring, August–September), water temperatures varied between 10.6 and 15°C, and conductivity was low (<120 µS/cm), except in Coldwater Creek, where conductivity was up to 255 µS/cm (Table 1).

Methods

Riparian vegetation, benthic leaf-litter composition, and shredder densities

Riparian-zone vegetation composition was surveyed along the 6 sites by recording % cover of different species of trees and shrubs in up to fourteen 10-m² quadrats randomly placed along the length of the sampling site on both stream banks. Species were identified using criteria of Williams et al. (1984) and Boland et al. (2006), and species were allocated to categories of native, camphor laurel, or other exotic. Five 30-cm² samples of benthic leaf litter were

collected randomly from each of 3 pools in each stream, to give a total of 15 samples. Samples of leaves and macroinvertebrates were collected into submerged plastic bags held downstream of a 30-cm² quadrat. In the laboratory, aquatic macroinvertebrates were removed from each sample and preserved in 70% ethanol for later identification and allocation to functional feeding groups. Identifiable leaves in each sample were separated into species, air-dried to constant mass, and weighed to the nearest 0.1 g.

Comparison of shredder densities on artificial leaf packs

To assess whether shredder densities differed between artificial packs of native (*C. serratifolia*) leaves and camphor laurel leaves incubated in each of the 6 streams, freshly abscised litter of both species was collected, air-dried to constant mass, and assembled into monospecific packs of 10 leaves each (Boulton and Boon 1991). Five packs of each leaf species were randomly placed in each of 3 pools in each stream (i.e., 2 leaf species × 6 streams × 3 pools × 5 replicates = 180 packs) and recovered after 14 d. In the laboratory, packs were dismantled under running water, and shredders were removed, counted, and identified. The associated leaf material was dried and weighed so that shredder densities could be expressed per g dry mass (DM). The dominant shredders were calamoceratid and leptocerid caddisflies, shrimps (*Paratya australiensis*), and the leptophlebiid mayfly *Atalophlebia*.

Growth of Anisocentropus larvae fed camphor laurel vs native eucalypt litter

The field survey and experiment revealed that *Anisocentropus*, a common shredder in these Orara River streams, still occurred in streams where camphor laurel dominated benthic leaf-litter composition. To assess the potential effects on larval growth of a diet consisting solely of camphor laurel, early *Anisocentropus* instars were collected from a stream with native riparian vegetation (Wayper Creek) and fed ad libitum freshly senesced leaf litter from camphor laurel leaves collected from infested Wongiwomble Creek. Because the dominant benthic leaf-litter species at Wayper Creek was *Eucalyptus grandis*, this species was used as the native food source in the comparative experiment rather than *C. serratifolia*. Larval size was measured as head width at its widest point (Álvarez and Pardo 2005, Rincón and Martínez 2006) using an ocular micrometer in a Stemi DV4 microscope (Zeiss, Sydney, Australia) at 32× magnification.

Four treatments were used to discriminate potential influences of the source stream water on *Anisocentropus* growth. Treatments were crossed combinations of

water source and leaf type (i.e., *E. grandis* vs camphor laurel in water from Wayper Creek [uninfested]; *E. grandis* vs camphor laurel in water from Wongiwomble Creek [infested]). The experiment began with 6 replicates of each of the 4 treatments. Each replicate consisted of 9 larvae in 2 L of aerated water from either Wayper or Wongiwomble Creeks, and larvae were fed either *E. grandis* or camphor laurel leaf litter. Three replicates were harvested at 21 d, and the remaining 3 replicates were harvested at 42 d. The harvesting was necessary because it was impossible to measure *Anisocentropus* larval head widths without removing the animals from their cases, and pilot studies revealed that larvae showed a marked reluctance to return to an abandoned case. To obtain initial head widths for larvae in each treatment (day 0), 4 sets of 9 larvae were randomly selected, preserved in 70% ethanol, and measured. Subsequently, head widths were measured for the samples from 21 and 42 d after preservation of the larvae in ethanol for an equivalent period (to avoid potentially variable shrinkage caused by different intervals since preservation).

Statistical analysis

A Kruskal–Wallis test was used to compare the median % covers of native, camphor laurel, and other exotic vegetation in the riparian zones of the 6 streams because arcsine \sqrt{x} transformation (Zar 1984) failed to normalize the data (based on Wilk–Shapiro normality tests). Pools were nested within streams that were triplicates within the fixed factor of riparian-zone vegetation (i.e., 3 infested streams, 3 uninfested). Therefore, a nested analysis of variance (ANOVA) was used to compare the mean proportions of camphor laurel leaf material in the benthic leaf-litter samples. The same analysis was used to compare mean shredder densities and densities of *Anisocentropus* larvae on the benthic leaf packs. For the infested streams, the densities of shredders and of *Anisocentropus* larvae in each pack from each stream were regressed against the % camphor laurel leaf litter in the packs to test the hypothesis that shredder densities would decline with increasing proportions of exotic litter. Reduced major axis (RMA) regression (Quinn and Keough 2002) was used to ascertain lines of best fit because the independent variable (% camphor laurel litter) was measured with error. Analysis of covariance (ANCOVA) was used to compare slopes and elevations of these lines among the 3 streams.

A nested ANOVA on transformed data was used to compare mean densities of total shredders and of *Anisocentropus* larvae found on artificial packs of native or camphor laurel litter after 14 d in infested

or uninfested streams. As before, pools were nested within streams. Mean imputation (Zar 1984) was necessary in several cases where packs were lost.

Mean head widths of *Anisocentropus* larvae in the 4 combinations of water source and diet were compared using 3-factor ANOVA (time with 3 fixed levels, water source with 2 fixed levels, litter type with 2 fixed levels). In this analysis, the interaction terms were of particular interest. If litter type rather than water source influenced growth rates, the time \times litter type interaction effect would be significant, whereas the time \times water source interaction effect would be nonsignificant. Differential survival in the treatments caused sample sizes of *Anisocentropus* larvae to differ among treatments by the end of the experiment. This difference necessitated type III calculations of the sums of squares (as recommended by Quinn and Keough 2002). Type III calculations use unweighted marginal means, and, hence, they are not influenced by sample size. All statistical analyses were done using Statistix (version 7.0; Analytical Software, Tallahassee, Florida).

Results

Riparian vegetation, benthic leaf-litter composition, and shredder densities

Thirty species of riparian plants were collected from across the 6 streams. Along the 3 infested streams, 70 to 90% of the canopy cover was camphor laurel (Table 1), and *Eucalyptus* spp., *C. serratifolia*, and the introduced Chinese privet *Ligustrum sinense* constituted the remaining dominant vegetation. Conversely, the 3 uninfested streams had a diverse canopy cover of native species, although the exotic shrub *Lantana camara* was present at all sites. The main native species along the banks of these streams included *C. serratifolia*, *F. coronata*, *Ceratopetalum apetalum*, *T. laurina*, the palm *Archontophoenix cunninghamiana*, and several species of eucalypt (Table 1). Much of the ground below the canopy along infested streams was bare, although patches of *L. sinense* and some ferns (*Adiantum diaphanum*, *Hypolepsis muelleri*) occurred in places. A much denser, species-rich ground cover carpeted the uninfested stream banks. Exotic grasses and small shrubs occurred at all the native sites but never constituted >10% of the total vegetation (Fig. 1). Percent cover of native vegetation was significantly higher in the uninfested Dingo, Poperaperan, and Wayper Creeks than in the infested creeks (Kruskal–Wallis, $H_{5,48} = 44.05$, $p < 0.001$), whereas the infested Coldwater and Karangi Creeks had lower % cover of exotic vegetation (other than camphor laurel) than the remaining 4 creeks (Fig. 1). No camphor laurel was

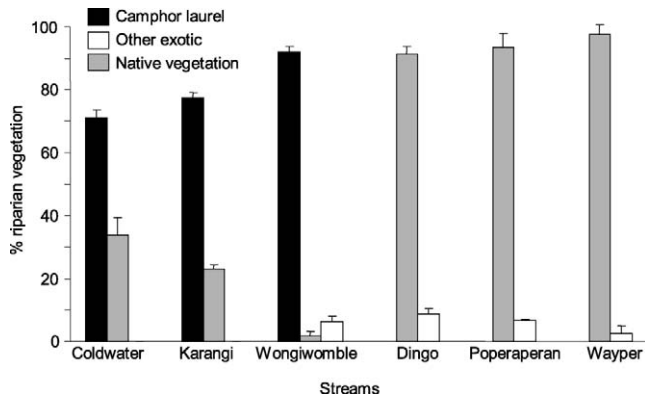


FIG. 1. Mean (± 1 SE) % cover of native vegetation, camphor laurel, and other exotic vegetation in the riparian zones of 6 Orara Valley streams.

recorded in the riparian zones of Dingo, Poperaperan, and Wayper Creeks.

No camphor laurel litter was found in leaf packs collected from the pools of uninfested streams. Camphor laurel litter constituted 60 to 83% of the leaf packs collected from pools in infested Coldwater and Wongiwomble Creeks but only 38 to 50% in leaf packs collected from pools in infested Karangi Creek (Fig. 2A), despite a riparian canopy cover of $\sim 80\%$ camphor laurel at Karangi Creek (Fig. 1). The remainder of the litter in the natural packs in Karangi Creek was mainly eucalypt leaves. Natural packs from Coldwater and Wongiwomble Creeks contained significantly more camphor laurel litter than did packs from Karangi Creek ($F_{4,72} = 6.81$, $p = 0.0001$; Fig. 2A). Median % camphor laurel leaf litter in natural leaf packs did not differ among pools within infested streams (nested ANOVA, $F_{12,72} = 0.67$, $p = 0.78$). Percent canopy cover of camphor laurel and % camphor laurel litter in the natural leaf packs were not related (cf. Figs 1 and 2A).

Median densities of shredders on natural leaf packs were significantly greater in uninfested compared to infested streams ($F_{1,72} = 31.78$, $p < 0.0001$; Fig. 2B). In uninfested streams, shredder densities did not differ among pools nested within streams but were significantly higher in Wayper compared to Poperaperan Creek ($F_{4,72} = 8.70$, $p < 0.0001$). Median shredder densities also did not differ significantly among pools within infested streams ($F_{12,72} = 1.35$, $p = 0.21$). Shredder densities were significantly higher in Karangi Creek, with $< 50\%$ camphor laurel litter in the natural benthic packs (Fig. 2A), compared to the other 2 infested creeks (Fig. 2B). *Anisocentropus* larvae occurred in all streams but, on average, were 20 \times more common in uninfested than in infested streams ($F_{1,72} = 125.71$, $p < 0.0001$; Fig. 2C). However, median densities did not differ among infested streams ($F_{4,72}$

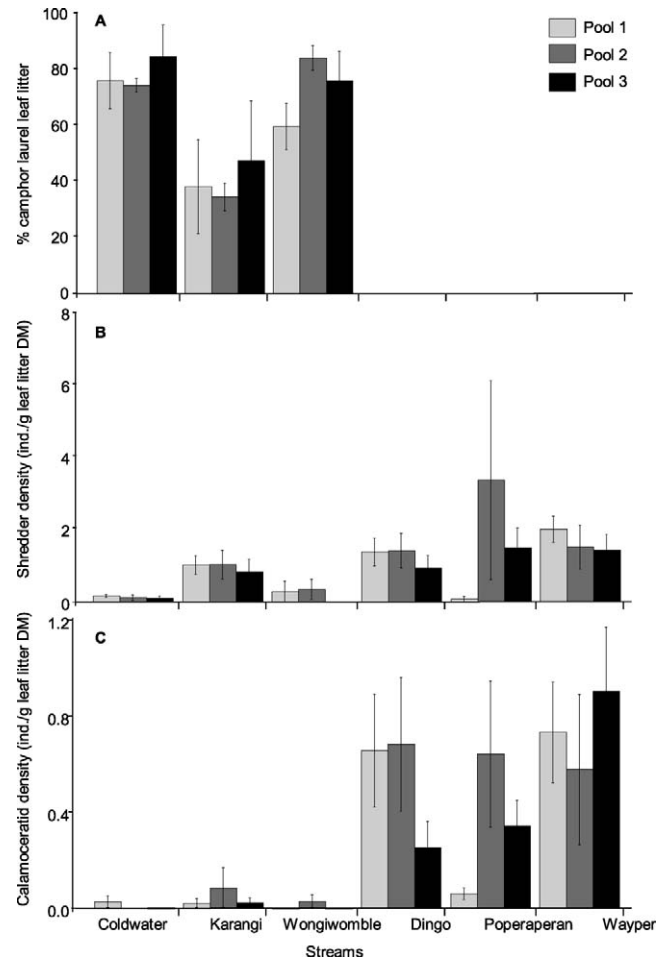


FIG. 2. Mean (± 1 SE) % dry mass of camphor laurel leaves (A), densities of shredders (B), and densities of *Anisocentropus* larvae (C) in natural leaf-litter packs from 3 pools along 6 Orara Valley streams.

$= 1.80$, $p < 0.14$) or pools nested within streams ($F_{12,72} = 1.28$, $p = 0.25$), probably because of the high variability in densities among packs (illustrated by the large standard error [SE] bars in Fig. 2C).

Densities of shredders were significantly negatively correlated with % camphor laurel leaf litter in natural packs in the 3 infested streams (RMA regression, $F_{1,43} = 12.46$, $p = 0.001$; Fig. 3). However, the association explained only 22.5% of the variance, and relationships were not significant when tested within individual streams. ANCOVA indicated that the slopes of these lines did not differ significantly ($F_{2,39} = 1.02$, $p = 0.37$) and could be explained by the common equation in Fig. 3. However, elevations of the lines differed significantly ($F_{2,41} = 7.70$, $p = 0.001$), and the y -intercept was greatest in Karangi Creek because of high numbers of shredders in the packs with low % camphor laurel leaf litter (Fig. 3). Shredders were

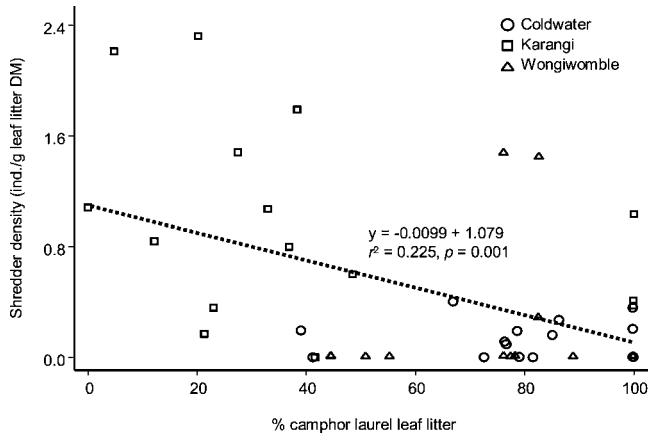


FIG. 3. Relationship between densities of shredders and % camphor laurel leaf litter in natural packs collected from 3 infested streams in the Orara Valley.

collected from packs that were 100% camphor laurel leaf litter (Fig. 3). No significant negative correlations were found between densities of *Anisocentropus* larvae and the % camphor laurel leaf litter in natural leaf packs across all streams combined ($p = 0.15$) or within individual streams ($p > 0.2$).

Comparison of shredder densities on artificial leaf packs

After 14 d, artificial packs of camphor laurel leaves placed in the infested streams supported the lowest median density of shredders (rank transformed data, $F_{3,144} = 13.76, p < 0.0001$) across pack types and stream types (Fig. 4A). Thus, our 1st hypothesis was supported: densities of shredders were greater on native litter than on camphor laurel litter in infested streams. Highest median densities of shredders occurred on native litter in uninfested streams (Fig. 4A), but densities on native litter did not differ significantly from densities on camphor laurel litter in infested streams. Thus, our 2nd hypothesis was not supported: densities of shredders were not lower on camphor laurel litter than on native litter in infested streams.

Within streams and within pools nested in streams, the differences in median densities of shredders on native and camphor laurel litter varied considerably. For example, in infested Coldwater and Wongiwomble Creeks, shredder densities were greater on native litter than on camphor laurel litter in all 3 pools (Fig. 4A). However, this trend was not consistent across the pools at Karangi Creek, where background levels of native litter were relatively high (Fig. 2A). In uninfested streams, the inconsistencies among pools were even greater. In 2 of the pools in Dingo Creek, significantly more shredders were found on native

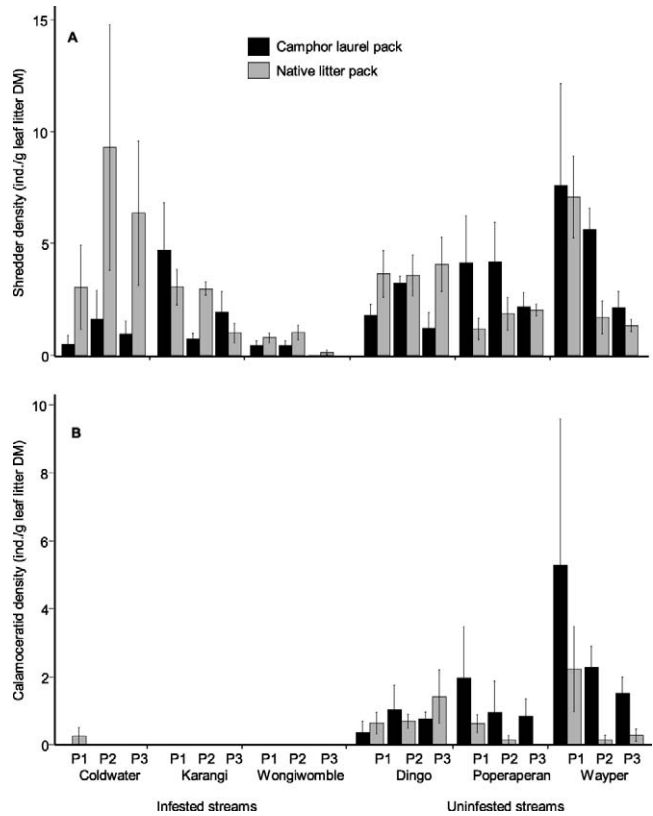


FIG. 4. Mean (± 1 SE) densities of shredders (A) and *Anisocentropus* larvae (B) on artificial monospecific packs of camphor laurel and of native *Callicoma serratifolia* leaf litter incubated for 14 d in 3 pools (P) along 6 Orara Valley streams.

litter, whereas densities did not differ among litter types in the 3rd pool. Conversely, in 2 pools in Poperaperan Creek and 1 pool in Wayper Creek, densities of shredders were significantly greater on camphor laurel than on native litter (Fig. 4A).

In infested streams, *Anisocentropus* larvae were absent from all artificial packs except native litter in 1 pool in Coldwater Creek (Fig. 4B). In the 3 uninfested streams, mean densities of *Anisocentropus* larvae were greater on camphor laurel than on native litter ($F_{1,72} = 4.86, p = 0.03$). However, the preferences varied significantly among streams ($F_{4,72} = 3.10, p = 0.02$). In Dingo Creek, mean densities did not differ between litter types, whereas in Poperaperan and Wayper Creeks, consistently more *Anisocentropus* larvae/g DM were found on camphor laurel than on native litter (Fig. 4B). Variation in densities among packs of the same litter type within pools was very high (large SE bars in Fig. 4B), and *Anisocentropus* densities did not differ significantly among pools nested within streams ($p = 0.60$).

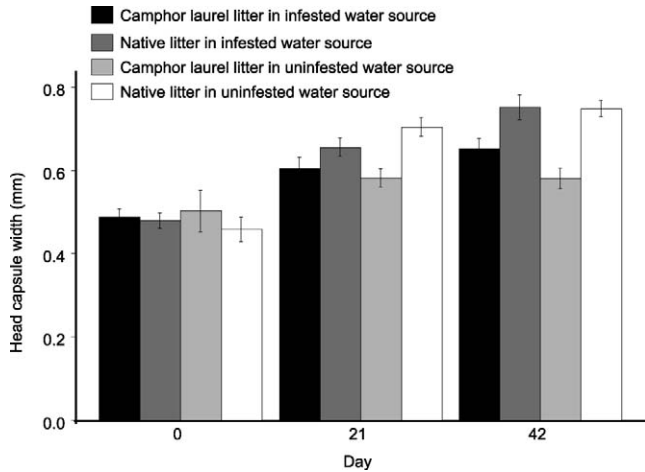


FIG. 5. Temporal changes in mean (± 1 SE) larval head widths of the calamoceratid caddisfly *Anisocentropus* reared in tanks of water from either an infested (Wongiwoomble) or uninfested (Wayper) water source and fed either camphor laurel or native eucalypt leaf litter.

Growth of Anisocentropus caddisfly larvae fed camphor laurel vs native eucalypt litter

When the experiment commenced, mean *Anisocentropus* head width did not differ among the 4 treatments ($p = 0.52$; Fig. 5). After 3 wk, mean head widths of larvae fed camphor laurel litter were significantly smaller than those of the larvae fed eucalypt litter, regardless of water source (i.e., from uninfested Wayper Creek and infested Wongiwoomble Creek), and this difference was even greater after 6 wk ($F_{1,199} = 15.07$, $p = 0.0001$; Fig. 5). Water source did not affect mean head width within litter types and days ($F_{1,199} = 0.32$, $p = 0.57$). The time \times litter type interaction effect was significant ($F_{2,199} = 6.4$, $p = 0.002$), but the time \times water source interaction effect was not significant ($F_{2,199} = 1.06$, $p = 0.35$), indicating that litter type rather than water source influenced larval growth rates. After 42 d, mean head widths of larvae fed camphor laurel in water from uninfested Wayper Creek appeared to be smaller than head widths of larvae fed camphor laurel in water from infested Wongiwoomble Creek (Fig. 5), but this difference was not statistically significant.

Frequency distributions of head widths within the 4 treatments over time (Fig. 6A–F) revealed some interesting subtleties in larval growth responses to different diets and water sources. Water source was not a significant factor affecting *mean* head width. However, after 3 wk on a diet of native litter, the frequency of larger larvae was higher in treatments with an uninfested water source (Fig. 6D) than in treatments with an infested water source (Fig. 6C).

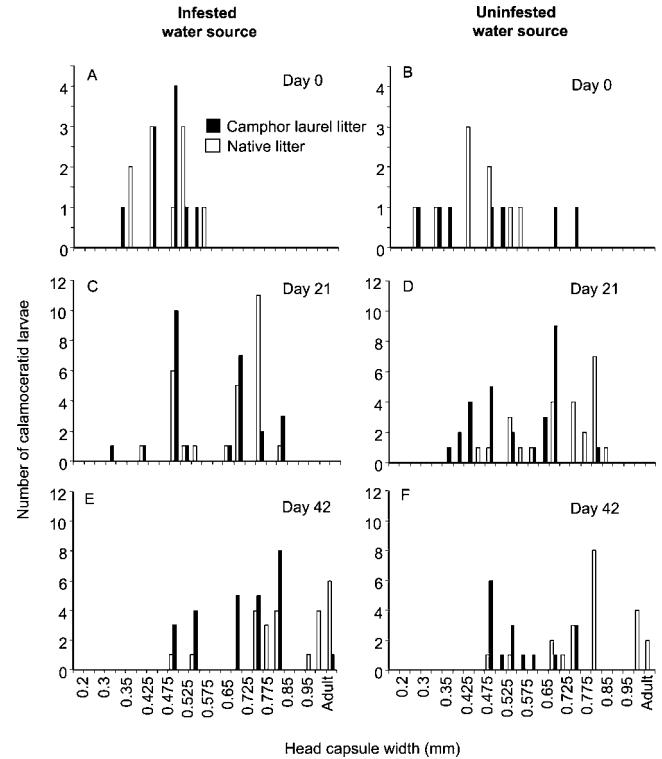


FIG. 6. Histograms of larval head widths of the calamoceratid caddisfly *Anisocentropus* reared on a diet of camphor laurel or native eucalypt leaf litter. Larvae were measured at the start of the experiment (day 0) (A, B) and after 21 d (C, D) and 42 d (E, F). Panels A, C, and E are treatments incubated in water from infested Wongiwoomble Creek; panels B, D, and F are treatments incubated in water from uninfested Wayper Creek.

After 42 d on a diet of camphor laurel litter, the frequency of small larvae (< 0.65 mm head width) was higher in treatments with an uninfested water source (Fig. 6F) than in treatments with water from an infested water source (Fig. 6E). Most important, after 42 d, only 1 *Anisocentropus* larva fed camphor laurel litter successfully emerged as an adult (Fig. 6E), whereas 8 larvae fed native eucalypt litter successfully emerged (Fig. 6F).

Discussion

Overall, our results indicate that the invasion of the riparian zones of subtropical streams in northern New South Wales by camphor laurel trees has had a detrimental effect on densities of native shredding invertebrates and impairs growth rates of a common shredding caddisfly. Negative effects of exotic leaf litter often have been demonstrated on stream invertebrate communities in temperate streams (Cortes et al. 1994, Abelho and Graça 1996, Bailey et al. 2001,

Albariño and Balseiro 2002, Reinhart and VandeVoort 2006), and this demonstration of an equivalent effect in Australian subtropical streams suggests parallel ecological responses between temperate streams and these subtropical streams. This finding supports the general contention that temperate and (sub)tropical streams do not always differ markedly in their ecology despite some environmental differences associated with latitude (review in Boulton et al. 2007), and it encourages cautious application of ecological models developed from data collected in temperate systems to tropical streams. At least in these Australian subtropical streams, shredding invertebrates apparently play a key role in leaf-litter processing and respond to differences in leaf quality in similar ways to shredders in forested temperate streams, and these results corroborate similar suggestions made by Graça et al. (2001) and Rincón and Martínez (2006).

Riparian vegetation, benthic leaf-litter composition, and shredder densities

Leaf-litter composition of naturally occurring benthic leaf packs did not closely match the species composition of the common riparian plant species in our study. This discrepancy was especially apparent at infested Karangi Creek, where riparian canopy cover of camphor laurel was 78%, yet camphor laurel leaves constituted only 38 to 50% of the leaf packs occurring in the stream pools. The assumption that benthic leaf-litter composition will reflect that of riparian-zone vegetation seems to be widely held, but factors such as variable rates and timing of leaf fall, differences in trapping efficiency and retention, and leaf breakdown dynamics (Webster and Benfield 1986, Quinn et al. 2000, Graça et al. 2001) contribute to this mismatch (Boulton and Boon 1991). Nonetheless, the validity of the comparison between infested and uninfested streams was supported by the absence of camphor laurel litter in leaf packs in uninfested streams.

Even in pools where camphor laurel constituted only 38 to 50% of the benthic leaf litter, the densities of native shredders were reduced compared to those on leaf packs devoid of camphor laurel litter in uninfested streams. Percent camphor laurel litter in benthic leaf packs and the shredder densities were significantly negatively correlated in the 3 infested streams. Camphor laurel leaves contain a rich cocktail of allelochemicals, aromatic oils, and other secondary compounds (Stubbs and Brushett 2001), and this chemical composition is a likely reason for the apparent avoidance of camphor laurel litter by many stream shredders. The inhibitory mechanism could be either direct toxicity to the invertebrates, reduction of

microbial colonization that supplements detritivore nutrition, or both. Polyphenols in many plant species inhibit microbial colonization of their leaf litter (Harrison 1971, Rosset et al. 1982), reducing the palatability of litter to most stream invertebrates (Bunn 1988, Graça 2001). Feeding experiments have demonstrated that the tropical shredding caddisflies *Nectopsyche argentata* and *Phylloicus priapululus* discriminate among leaf species and different microbial conditioning times (Graça et al. 2001), and another experiment has shown that the tropical *Phylloicus* reject leaves with high concentrations of polyphenols (Rincón and Martínez 2006). Tannins leached from Chinese tallow (*Sapium sebiferum*) leaves directly inhibited the feeding rate of 2 aquatic detritivores in Texan ponds (Cameron and LaPoint 1978), demonstrating a strong relationship between leaf chemistry and feeding behavior in some species.

Despite the negative correlation of shredder density and % camphor laurel leaf litter in natural leaf packs in our study, shredders were collected from packs composed entirely of camphor laurel litter in all 3 infested streams. *Anisocentropus* larvae had cut material from many of the leaves in these packs and used it to construct their cases. The toughness of the leaf blades and their resistance to microbial decay probably contribute greatly to their quality as case-building material, and this shredding activity is likely to be a significant pathway in camphor laurel litter breakdown in these streams. In an experiment on feeding preferences, *Phylloicus* made cases out of leaves of *Anacardium*, a species rich in lignin and polyphenols, yet fed on *Ficus* leaves, which had more nutrients and less polyphenols than *Anacardium* (Rincón and Martínez 2006). In an Australian tropical stream, *Anisocentropus kirramus* selected relatively tough leaves for case construction and used species that were not preferred as food (Bastian et al. 2007). Feeding rates and fitness of the shredder *Anisocentropus maculatus* in Hong Kong were adversely affected by leaf toughness, and larval mortality was >7× higher for animals fed tough leaves compared with softer ones (Li and Dudgeon 2008).

Many stream invertebrates also use leaf litter for shelter and habitat (Minshall 1984, Richardson 1992). It is also possible that some of the shredders in these subtropical streams are pre-adapted to dealing with physically tough leaves rich in secondary compounds. For example, native riparian eucalypt litter is rich in secondary compounds (Macauley and Fox 1977, Bärlocher et al. 1995) and sclerophyllous, yet it is shredded by many native species of Australian stream invertebrates (Bunn 1988, Boulton 1991, Yeates and Barmuta 1999). The riparian zones of most tropical streams support native plant species that shed litter

containing polyphenols, other tannins, and even alkaloids (Covich 1988, Stout 1989, Graça et al. 2001, Rincón and Martínez 2006), so it is predicted that some native detritivores would have co-evolved to be able to feed on this litter successfully (Wantzen et al. 2002).

Comparison of shredder densities on artificial leaf packs

Given the apparent negative effect of camphor laurel on shredder densities in our survey, we hypothesized that lower densities of shredders would occur on camphor laurel than on native litter in experimentally introduced monospecific packs in these streams after 2 wk (judged to be an appropriate time for invertebrate colonization and microbial conditioning but before significant litter breakdown; Rowe and Richardson 2001, Mathuriau and Chauvet 2002). In infested streams, median densities of shredders were significantly lower on camphor laurel litter than on native litter. This result implies that a positive response by native shredders to riparian restoration by removal of camphor laurel trees is likely in these particular streams and that native shredders have not made an irreversible switch in leaf preference from *C. serratifolia* to camphor laurel. This information is crucial when planning restoration activities because it validates a proposed mechanism by which the restoration is predicted to benefit the ecosystem, a criterion suggested by Jansson et al. (2005) to supplement other measures of the ecological success of river restoration (Palmer et al. 2005).

Unexpectedly, shredder densities did not differ between camphor laurel and native litter packs after 14 d in the 3 uninfested streams. A large proportion of the shredders on the camphor laurel leaf packs in these streams was *Anisocentropus* larvae, and many were actively cutting cases. Their mean densities were greater on camphor laurel than on native litter in the pools in Poperaperan and Wayper Creeks, but densities did not differ in Dingo Creek, where eucalypt litter was especially abundant and might have provided an alternative source of case material. The differences in densities of both total shredders and *Anisocentropus* larvae between leaf types also varied considerably at the scale of individual pools within these streams. This variability in response implies contributions from other factors, such as background variation in nearby native leaf-litter quality and quantity (Bastian et al. 2007), as well as specific interactions among different shredders. In the uninfested streams, where overall shredder densities were much greater than in infested streams, competition for leaf resources might be intense. Intraspecific interference among tropical Australian shredders (including

Anisocentropus) has been demonstrated experimentally and results in lower breakdown rates per capita of shredding invertebrate (Boyero and Pearson 2006). *Anisocentropus* is capable of directly interfering with nearby calamoceratid larvae by feeding on their cases (Boyero and Pearson 2006, JND, personal observation).

Growth of Anisocentropus larvae fed camphor laurel vs native eucalypt litter

Most studies of the potential effects of exotic riparian vegetation on stream invertebrate assemblages have focused on changes in community composition, diversity, and abundance (e.g., Abelho and Graça 1996, Royer et al. 1999, Quinn et al. 2000, Bailey et al. 2001, Sampaio et al. 2001, Reinhart and VandeVoort 2006). The potential sublethal effects of exotic vegetation on growth rates or success of emergence of hemimetabolous aquatic insects are assessed less commonly (Smock and MacGregor 1988, Quinn et al. 2000, Graça et al. 2001, Li and Dudgeon 2008). In our study, *Anisocentropus* larvae fed only camphor laurel grew more slowly over 42 d than larvae fed native eucalypt litter. Furthermore, only 1 larva in the camphor laurel litter treatment successfully emerged as an adult after 6 wk compared to 8 adults in the native litter treatment. The reduced growth rate on camphor laurel litter probably reflects its poorer food quality compared to that of the native eucalypt litter. The principal ecological implication of this growth experiment is that secondary production of detritivores, such as this common caddisfly, is potentially reduced in streams where camphor laurel litter constitutes most of the available organic matter, with negative repercussions for higher trophic levels such as predatory fish and aquatic invertebrates. Similar conclusions have been drawn from other studies where growth rates of shredders have been lower on exotic compared to native litter (Smock and MacGregor 1988), highlighting the severity of the likely impacts of marked changes in the species composition of riparian-zone vegetation.

Most studies of the feeding biology of shredding caddisflies report faster growth on leaf species that either decompose more rapidly (i.e., softer structural tissue, greater nutrient concentrations) or that are favored by shredders in the natural environment (Canhoto and Graça 1995, Hutchens et al. 1997, Quinn et al. 2000, Graça et al. 2001, González and Graça 2003, Bastian et al. 2007). However, some aquatic detritivores can increase their feeding rates on low-quality leaf litter to compensate (Anderson and Cummins 1979, Friberg and Jacobsen 1999, Li and Dudgeon 2008). No evidence was found for this compensatory

behavior in our experimental study, and *Anisocentropus* growth rates were significantly lower on the exotic camphor laurel litter than on native litter. Moreover, no evidence was found for any effect of the source of water (i.e., whether from an infested or an uninfested stream) on mean head widths of *Anisocentropus* larvae after 42 d. Our experiment was designed to isolate any potential effect that dissolved leachates from litter in camphor laurel-infested streams might have had on growth rates of *Anisocentropus* larvae because some authors have reported effects of poor water quality on shredder development and growth (reviews in Abelho 2001, Graça 2001). After 21 d, some variability that was potentially associated with water source was observed in the frequency distribution of larval size, but this variability was inconsistent and was not evident at the end of the experiment.

In an experiment similar to ours, Rincón and Martínez (2006) fed leaf discs of 2 tropical riparian plants to *Phylloicus* from northwestern Venezuela and assessed their growth rates. Initial head widths were highly variable in the experiment because larval availability was low, and the authors interpreted this initial variability as masking differences in growth rates (Rincón and Martínez 2006). Rincón and Martínez (2006) did not present information on differences in successful emergence of adults fed on the different diets. Nonetheless, this calamoceratid was able to discriminate among leaf species for case material and preferred food (Rincón and Martínez 2006). In a comparison of feeding behavior by 2 species of tropical shredding caddisfly, Graça et al. (2001) found no evidence for selection of native leaves over exotic leaves—indeed, the tropical caddisflies in their study preferred the exotic leaves of *Alnus glutinosa*. Furthermore, native leaves were not a better food source than exotic ones for the 2 shredders (Graça et al. 2001). In studies by Graça et al. (2001) and Bastian et al. (2007), the degree of microbial conditioning seemed to play a greater role than leaf species in leaf-litter preference by shredding caddisflies.

Our experiment did not run long enough to indicate whether overall success of adult emergence was significantly reduced for larvae fed solely on camphor laurel, but the lower emergence rate suggests that recruitment of this common caddisfly is inhibited in infested streams. Given the relatively short period of invasion by camphor laurel in these New South Wales streams, the cumulative effects of reduced recruitment might not yet be evident as local extinction of species, such as *Anisocentropus*. In many cases where exotic riparian vegetation has invaded streams, detritivore species composition has changed substantially. For example, large shredders, such as the stonefly *Klapop-*

teryx kuscheli and the caddisfly *Parasericostoma cristatum*, which were common on native mountain beech packs, were not found on packs of exotic pine litter in Patagonian streams (Albariño and Balseiro 2002). In another study comparing invertebrate assemblages on native cottonwood and introduced salt cedar in a small Arizonan stream, Bailey et al. (2001) found a more diverse community and >4× more individuals on the native leaf litter than on the introduced litter. Nonetheless, significant differences in aquatic invertebrate densities (e.g., Royer et al. 1999) or leaf species preferences by native stream fauna (Parkyn and Winterbourn 1997) are not always found between exotic and native leaf litter, and responses to invasion of the riparian zone by exotic trees can be highly location-specific and quite subtle (Larrañaga et al. 2006).

Marked reductions in abundances of entire functional feeding groups, such as shredders, that facilitate the essential ecosystem service of organic matter breakdown could have severe implications in subtropical streams where riparian zones are being invaded by camphor laurel. One likely outcome of the reduced shredding activity by aquatic invertebrates is accumulation of dense packs of camphor laurel litter resulting in high concentrations of leachates in the water and low dissolved O₂ during low-flow periods (JND, unpublished data), rendering the environment inimical for most aquatic life. Over time, the effects of this decline in water quality could eliminate populations of potential colonists even if camphor laurel could be removed from the riparian zone. In the streams in our study, the ecological success of camphor laurel removal probably could be assessed from shredder densities on benthic leaf packs, supplemented with measures of the population dynamics of *Anisocentropus*, such as growth rate or success of adult emergence. These latter measures are more time-consuming to obtain than shredder densities, but they will better illustrate subtle population responses and sublethal effects, and they should detect changes at a finer resolution than might result from simply measuring total shredder densities. We conclude from our study that shredders, such as calamoceratid caddisfly larvae, might prefer camphor laurel litter for case construction—a great house—yet find it such a poor food source that, in time, recruitment and secondary production might be so impaired that local extinctions will occur in these infested subtropical streams.

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