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Selectivity of a biological control agent, *Diorhabda carinulata* Desbrochers, 1870 (Coleoptera: Chrysomelidae) for host species within the genus *Tamarix* Linneaus, 1753

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Abstract. Initial field releases of the saltcedar leaf beetle, *Diorhabda carinulata* Desbrochers, 1870 (Chrysomelidae), against saltcedars, *Tamarix* Linneaus, 1753 (Tamaricaceae) in North America were unsuccessful at sites where the target taxon was *T. parviflora* de Condolle, 1828 as opposed to the more widespread *T. ramosissima* Ledebour, 1829 and related forms. A series of field and greenhouse studies was conducted to determine the basis for these failures. Generally, *T. parviflora* was a suitable host for larval and adult development. Larval growth was not significantly affected by host species although developmental rate was slightly slower when fed *T. parviflora* vs. *T. ramossisima*; nitrogen enrichment had greater influence on growth than did host identity. Insect feeding impact to *T. ramossisima* outplanted to the field was initially three times greater than to matched *T. parviflora* plants, apparently as a consequence of adult oviposition preference. Subsequent larval migration from defoliated to green plants resulted in roughly equivalent defoliation of both hosts. Where the two *Tamarix* species co-occurred in northern Nevada, the 'preference' for *T. ramossisima* was apparent because it was consistently more heavily colonized, and utilization of *T. parviflora* declined as insect densities diminished. These results, and the lack of alternative explanations for establishment failures at *T. parviflora* sites (predation, developmental constraints, climate conditions), lead to the conclusion that such failures are based on host specificity as a consequence of adult behavioral avoidance of *T. parviflora*. They also suggest that risks to non-target plants both within the genus *Tamarix* (e.g., *T. aphylla* (Linneaus) Karsten, 1882) and in a related family (Frankeniaceae: *Frankenia* spp.) are low and should not delay program implementation.

Key Words. Invasive species, biological control, plant-herbivore interactions, host specialization, *Tamarix*, *Diorhabda*.

Introduction

The introduction of novel herbivores to suppress weeds is an important element in the management of invasive species, but it is also fraught with complexity (Sheppard & Raghu 2005). A good candidate agent for classical biological weed control (biocontrol) is one with a narrow host range, yet sufficiently robust in its biology to be effective under a variety of circumstances in which control is desired. Oftentimes the target consists of a suite of related invasive taxa, such as species within one or two genera (e.g., *Carduus* or *Cirsium* (Asteraceae), Zwolfer & Harris 1984; *Centaurea* (Asteraceae), Muller-Scharer & Schroeder 1993), and while not essential, it is preferable and cost-effective if the agent has substantial impacts on all forms from the weed group.

Breadth in host utilization is not, however, desirable if it extends to non-target taxa, particularly native or economic species closely related to the target weed (McEvoy 1996, Louda et al. 2003). For example, *Rhinocyllus conicus* Froelich, 1792 (Curculionidae), a flowerhead weevil introduced to control musk and other weedy

thistles, is also known to feed on North American native thistles of conservation concern (Arnett & Louda 2002). Still, there is ample evidence of introduced agents selectively using target species without unacceptable impact to non-target congeners. *Aphthona* Chevrolat, 1837 flea beetles introduced to control leafy spurge (*Euphorbia esula*, Euphorbiaceae) show little tendency to use native species of *Euphorbia* (Pemberton 1985, Gassmann 1996, Baker et al. 2003) and *Galerucella* Crotch 1873 leaf beetles appear specific to their target purple loosestrife (*Lythrum salicaria* Linneaus, Lythraceae), despite presence of other *Lythrum* species in the introduced range (Blossey et al. 2001). There are several examples of selectivity by specialist herbivores within a host species, such as differential use of *Phragmites australis* (Poaceae) haplotypes (Lambert et al. 2007) or genetic forms of *Chondrilla juncea* (Asteraceae) (Cullen & Moore 1983), *Melaleuca quinquenervia* (Myrtaceae) (Dray et al. 2004), and *Schinus terebinthefolius* (Anacardiaceae) (Manrique et al. 2008). The avoidance of some congeners by a candidate agent is presumably a desirable trait indicating that the anticipated level of specificity is probably realistic, and thus its introduction is acceptable for weed control.

A problem for biocontrol development arises because there can be discrepancies between how a candidate agent responds to potential hosts in controlled environments and how it performs when released into the field. In host range testing under laboratory conditions, herbivores often show greater range in physiological capacity to use non-target plants than is observed under field conditions, possibly because the artificial nature of experimental forced feeding results in atypical behavior, or starvation and placement onto a plant causes feeding even though stimulatory cues to induce feeding are not present (Sheppard & Raghu 2005). This is a basic dilemma of biocontrol testing, in that a good candidate may be rejected unnecessarily because of its atypical performance in quarantine, and for safety or regulatory reasons more reliable field tests cannot be conducted. Improved reliability may come from detailed measurements in tests, such as going beyond simple observations of feeding, location and survival to assessing growth rates or quantifying behavioral responses on potential hosts (Louda et al. 2003). However, the ecological meaningfulness of laboratory results is limited, and it is often observed that as the realism of experimental conditions is increased, the range of host utilization is reduced and the reliability of the test results seems to be enhanced (Kaufman & Landis 2000, Dudley & Kazmer 2005, Uygur et al. 2005, Pratt et al. 2009). It is difficult to create quarantine-level conditions that replicate natural systems, and impractical to test every genetic form of biocontrol agent against every conceivable non-target prior to release of candidate agents. Thus, we must use whatever reasonable data are available, cautiously extrapolate results from some host-herbivore trials to other related organisms or conditions, and glean information retrospectively where possible so that future expectations can be refined.

The development since the 1980s of biocontrol for invasive saltcedar [*Tamarix* spp. Linneaus, 1753 (Tamaricaceae); a.k.a. tamarisk] in western North America has had variable success for a variety of reasons, some biological while others are related to a very cautious regulatory environment (DeLoach et al. 2004, Dudley & DeLoach 2004). The initial concern was that *Tamarix* control would reduce habitat for the endangered southwestern willow flycatcher [*Empidonax traillii extimus* (Tyrannidae)]. More recently, it was postulated that biocontrol agents pose risks to non-target plants, specifically an evergreen congener, *T. aphylla* (Linneaus) Karsten, 1882

or athel, used horticulturally in arid regions (Milbrath & DeLoach 2006a, b; Moran et al. 2009), and distantly-related halophytes of the genus *Frankenia* Linneaus (Lewis et al. 2003, Dudley & Kazmer 2005, Herr et al. 2009).

Following extensive testing, we conducted numerous research releases of the northern tamarisk leaf beetle (*Diorhabda elongata deserticola* Chen, 1961 [= *D. carinulata* Desbrochers, 1870) of Tracy & Robbins (2009)] in seven states, first into cages in 1999 (Dudley et al. 2001) followed by open releases in 2001; most did not result in establishment (DeLoach et al. 2004). Several ecological factors may explain failures, including inappropriate developmental responses related to latitude (Bean et al. 2007) and invertebrate predation (Herrera 2003, DeLoach et al. 2004). Other species and ecotypes within the *D.* '*elongata*' complex from different latitudes have been tested to determine if they perform better at latitudes where the original populations failed (Dudley et al. 2006, Dalin et al. 2010).

These factors are, however, insufficient to explain failures at sites where *T. parviflora* de Condolle, 1828 was the invasive form of saltcedar rather than the more common *T. ramosissima* Ledebour, 1829 and its genetic variants. Both species are named as targets for biocontrol (DeLoach et al. 1996, Richard 2003). They differ somewhat in growth form and phenology and generally infest different geographic regions but do co-occur (Baum 1967, Dudley & Collins 1995). Laboratory utilization of these two taxa by *D. carinulata* can differ somewhat (Lewis et al. 2003), and observations of less vigorous feeding and growth when fed *T. parviflora* in culture (D. Bean personal observation) suggested that in the open field, differences in host plant suitability may have contributed to establishment failures. This report documents such interactions from controlled laboratory experiments and field studies with these two target taxa, with additional information on *T. aphylla* and its hybrid forms. If host specialization does differ within the genus *Tamarix*, the implications for the biocontrol program may infer that risks to other non-targets, such as *T. aphylla* and *Frankenia* spp., may be lower than anticipated. This report includes several related but distinct studies, so for coherence the methods and results for each are presented together.

Study Organisms

Tamarix parviflora, *T. ramosissima*, and *T. chinensis* Loureiro, 1790 are deciduous, large shrubby forms of saltcedar, unlike *T. aphylla*, an evergreen arboreal species. *Tamarix ramosissima* and *T. chinensis* are derived from central Asia and are now abundant throughout the arid and semi-arid western U.S.A. (Baum 1967, Friedman et al. 2005, Gaskin & Schaal 2003). Both are 5-petaled *Tamarix* species and it is difficult to distinguish between the two, and although there is little indication of hybridization in Asia they have hybridized extensively in North America, making the distinction between species even more unclear (Gaskin & Schaal 2002, 2003). Most infestations in the western U.S.A. represent a hybrid complex between *T. ramosissima* and *T. chinensis* with genetic introgression resulting in mixed representation of each genome in approximately 80% of North American plants tested (Gaskin & Kazmer 2009). Field studies indicate that *D. carinulata* did not differentiate among plants derived from these hybrid forms (Moran et al. 2009) so for these studies the *T. ramosissima* × *T. chinensis* complex will be referred to collectively as *T. ramosissima. Tamarix parviflora* is a 4-petaled species from the eastern Mediterranean region (Baum 1967) and has a more limited invasive range in

North America, primarily in central and northern California (Dudley & Collins 1995). It does occur adventively in other ecosystems including the Walker River in Nevada, coastal and desert valleys of southern California, the Virgin River and other lower Colorado River locations, and the Rio Grande Valley in New Mexico, often in loose association with *T. ramosissima*.

The other form of *Tamarix* in this study is *T. aphylla*, which is largely restricted to areas of the southwestern U.S.A. and northern Mexico without sustained temperatures below freezing. It was originally thought to be non-reproductive in North America despite its invasive nature in Australia (Griffin et al. 1989), but recent evidence shows that *T. aphylla* can produce viable seed in some southwestern locations (Walker et al. 2006). It also hybridizes with the deciduous forms of saltcedar in the same areas (Gaskin & Shafroth 2005).

During infrequent hydrological conditions with good moisture and low competitor densities *Tamarix* spp. can form extensive populations adjacent to rivers and wetlands (Brotherson & Field 1987, Shafroth et al. 2005). Impacts are presumably similar, but those of *T. ramosissima* are more widespread and detrimental to riparian ecosystems and resource values; these impacts are described elsewhere (Lovich & de Govenainen 1998, Dudley et al. 2000, Shafroth et al. 2005). Prior to biocontrol introductions there were few arthropods that fed on any forms of *Tamarix*, except for an unintentionally introduced leafhopper, *Opsius stactogalus* Fieber, 1866 (Homoptera: Cicadellidae) and a scale insect, *Chionaspis* Signoret, 1868 (Homoptera: Diaspididae). Both insects feed exclusively on *Tamarix* and occasionally achieve high densities that can damage host plants (Wiesenborn 2005, Liesner 1971), as can a more recently detected weevil, *Coniatus* Germar, 1817 (Curculionidae) (Eckberg & Foster 2011, Dudley & Bean 2012).

The tamarisk leaf beetle, *D. elongata* (sensu lato), is associated almost exclusively with *Tamarix* spp. in the Old World, with minor occurrence on another genus in the Tamaricaceae, *Myricaria* Desvaux, 1825 (but not the other confamilial genus *Reaumuria*, Linneeaus, 1759) (Kovalev 1995, DeLoach et al. 1996, Richard 2003). Its relationship with specific taxa within the *Tamarix* genus is not well established (Tracy & Robbins 2009). Several ecotypes from five subspecies, now elevated to species status (Tracy & Robbins 2009) comprise the *D.* '*elongata*' complex, all of which share similar physical and ecological traits and were evaluated for genetic relatedness and non-target plant use (Bean et al., in press, Milbrath & DeLoach 2006b, Dalin et al. 2009, Herr et al. 2009). The original population evaluated for introduction, *D. e. deserticola* (nomenclature changed to *D. carinulata*) from central Asia, showed traits conducive to biocontrol introductions [host specificity, substantial host impact, and ease of handling], and was found to cause defoliation of *T. ramosissima* in parts of central Asia (Sha & Yibulayin 1993, Li et al. 2000). Following standard host-range testing, *D. carinulata* was originally approved for release to control saltcedar in 1996. The controversy over southwestern willow flycatcher nesting delayed open field introductions until 2001, following two years of field cage research testing at a series of sites in western states where this bird does not nest in *Tamarix* spp. (Dudley et al. 2001). Other species and ecotypes of *Diorhabda* Weise, 1883 have been released in some states and against various *Tamarix* forms (Tracy & Robbins 2009, Dalin et al. 2010), but an ecotype of *D. carinulata* from Fukang, China is the most widely distributed agent for biocontrol of *Tamarix* spp. (Tracy & Robbins 2009) and is the subject of this study.

Methods and Results

Study 1—Field Cage Performance Based on Host Species

The pre-release field cage trials comprise the first element of this study, and were intended to determine whether *D. carinulata* could develop, reproduce and survive through winter in regions where weed control was desired. Eleven sites in six states were used for testing, the primary differences between sites being geography, climate and host species. Of the 11 sites, most were infested with the *T. ramosissima* form of tamarisk, while three sites in the interior Coast Range of California were occupied by *T. parviflora*: Cache Creek (Yolo County: 38.69°N, 121.93°W), Bear Creek (Colusa County: 39.00° N, 122.36° W), and San Antonio Creek (Monterey County: 35.90°N, 121.09° W).

In spring of 1999, one to three large cages were placed over existing, mature *Tamarix* plants at each site (Dudley et al. 2001). Cages varied in dimensions from 11 m^3 to 28 m^3, depending on materials available to co-operating researchers, but were to provide similar conditions into which *D. carinulata* was introduced. Approximately 200 lab-reared adults, and in some cases larvae as well, were released inside the cages in early summer. Insects were monitored ca. twice monthly at all sites, counting numbers of each stage on four pre-selected branches to yield an estimate of abundance and dynamics of growth and development. Percent defoliation owing to herbivory was also estimated visually on the same branches. In-cage establishment was successful if over-wintering adults emerged the following spring; if no spring emergence occurred, adults and sometimes larvae were re-introduced into those cages, sometimes several times during the season. Here we report results from cages at the three sites infested by *T. parviflora*, along with two *T. ramosissima* sites, and compare with overall results from all sites as reported by DeLoach et al. (2004).

Reproduction by *D. carinulata* occurred at all three *T. parviflora* test sites during the season following release, but at none of the sites was more than a single generation produced, and population growth was anemic. At the San Antonio Creek site two over-wintering adults were encountered in January in the litter beneath the caged plant, but no emergence was observed at any site the following spring. Beetles from other, more successful sites were re-stocked into cages in 2000, but again failed to thrive and establish (Fig. 1). No further releases were attempted of this form of *Diorhabda*. Despite repeated herbivore introductions during the 2000 growth season, foliar damage on the marked stems at Bear Creek reached almost 20% on one sampling date but was ca. 4% for most of the time insects were present. Impact was approximately 40% for a short period at San Antonio Creek but foliage recovery was rapid and no further damage occurred, while no significant damage was done by beetles at Cache Creek.

Beetles established and successfully over-wintered in cages at 6 sites where the target taxon was *T. ramosissima* (Fig. 1 represents two of those sites in California and western Nevada), and often achieved nearly 100% defoliation of caged plants (DeLoach et al. 2004). The decline in abundances (Fig. 1) reflect descent into the litter following diapause induction. A single generation was observed at the Owens Valley site prior to diapause, while two peaks for the Walker Lake site corresponded to two cohorts produced. All successful *T. ramosissima* sites were north of 38° N latitude, and insects were released into the open at these sites in 2001. Although at

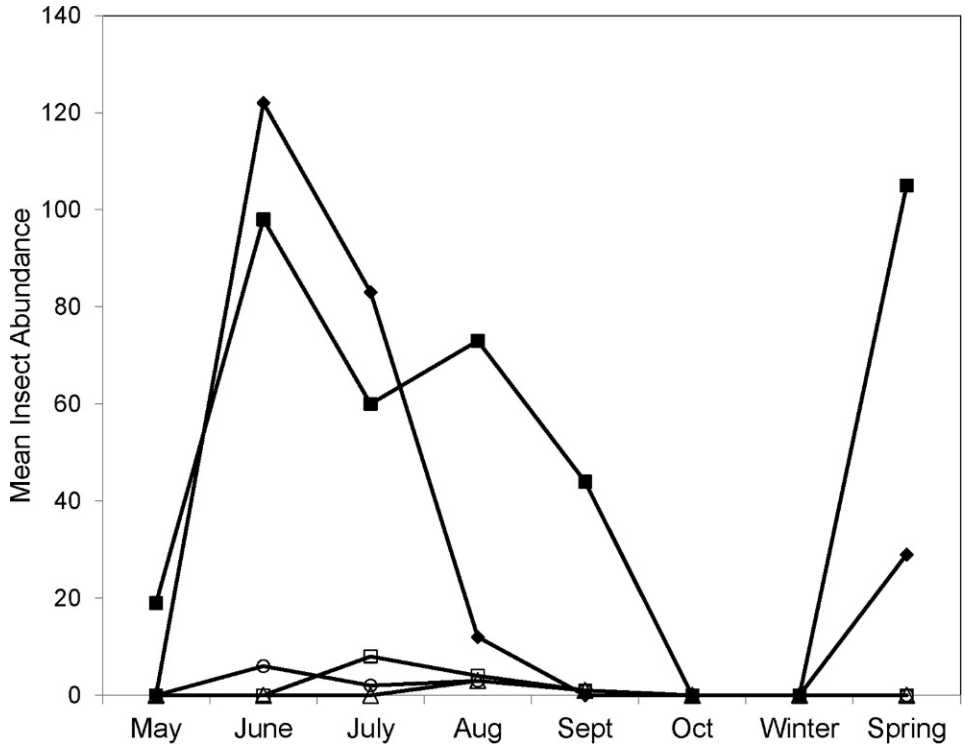

Figure 1. *Diorhabda carinulata* population establishment in cage trials at sites with *T. parviflora* as the target host (Bear—○, Cache—□, San Antonio—Δ) or *T. ramosissima* (Walker—▲, Owens—■). Data points represent maximum mean adult abundances on marked branches during each month of the growth season, and subsequent numbers in spring following winter diapause.

some sites subsequent field establishment was unsuccessful (e.g., Owens Valley), this was typically owing to premature reproductive diapause imposed by daylength at southern locations or because arthropod predators appeared to be an overriding factor limiting establishment (DeLoach et al. 2004, Bean et al. 2007).

Study 2—Container Plant Experimental Trials

Two tests were conducted rearing *D. carinulata* in sleeves on potted plants, and comparing growth, development and survival on *T. parviflora* vs. *T. ramosissima*. Plants were grown from cuttings, first rooted in water then transferred to a low nutrient substrate (one part commercial potting soil and 3 parts sand/silt material) in 2-gallon plastic containers. Plants generally ranged from 3 to 6 dm tall, each was enclosed in nylon mesh sleeve secured by wire ties at the plant base and above, and insects were introduced into the sleeves.

The first test was conducted at a University of California greenhouse in Berkeley, California. This trial was also designed to test the influence of salt and nitrogen augmentation on insect performance. These treatments were created by adding 20 mg of sodium nitrate ($NaNO_3$) bi-weekly directly to container soil for 2 months, or one gram of sea salt to the individual tray that each container sat in (and was used for watering from below to simulate normal field uptake). This was conducted as a 3-way cross-factorial design, with addition of N, salt or both for each *Tamarix* species

Table 1. Effect of host species, salt and nitrogen on development of *D. carinulata* in greenhouse trials. Days to pupation is the mean number of days to reach the pre-pupal stage following the first day of pupal development in any treatment. Superscript letters indicate treatment pairs that do not differ by multiple range test. Bottom rows show ANOVA results for main effects and for the only significant interaction ($P < 0.05$).

	Days to pupation	
	T. ramosissima	*T. parviflora*
Control	6.5 (0.6)[b]	6.3 (0.9)[b]
Salt	5.2 (0.25)[b]	7.0 (1.1)[b]
Nitrogen	3.0 (0.1)[a]	3.7 (0.3)[ac]
N + salt	2.2 (0.2)[a]	5.0 (0.6)[bc]
Species	$F = 7.47$, $P < 0.02$	
Nitrogen	$F = 36.83$, $P < 0.001$	
Salt	n.s.	
Species × salt	$F = 4.80$, $P < 0.05$	

along with controls that received no augmentation but were otherwise maintained the same. Each block of treatments was replicated five times, yielding a total of 40 container plants. Twenty first-instar larvae were transferred into each sleeve at one or two days old during the first week of August 2002. Those completing all three larval stages were collected as they prepared to pupate; pre-pupae were identifiable as such when they ceased feeding and descended to the lower part of the sleeve where they displayed a characteristic curled pre-pupal posture. Sleeves were checked twice daily to detect entry to this stage. Pre-pupae were dried 24 h at 50°C and weighed on an electrobalance to determine maximum biomass achieved. Biomass, percent survival and days to reach the pre-pupal stage were calculated as means for each replicate container plant, and these values were analyzed using 3-way ANOVA to test effects of nutrient, salt and host species treatments and possible interactions among these factors.

The second trial was conducted in outdoor wading pools in Lovelock, Nevada. This location was near the field study site on the lower Humboldt River, so shared climatic conditions with the ''natural'' habitat. This trial tested the influence of *Tamarix* genotype on insect growth, including two additional taxa—the evergreen *T. aphylla* and a hybrid between it and *T. ramosissima*. This unusual hybrid has been reported from several locations (Walker et al. 2006, Gaskin & Shafroth 2005), including Lake Mead, Nevada where cuttings of both genetic types were collected. Five blocks of each treatment (*T. parviflora* from Cache Creek, California; *T. ramosissima* from the Humboldt River, Nevada; and the two *T. aphylla* types) were prepared, two blocks in each of two plastic wading pools, and a fifth in a third pool. Irrigation was thus from below, and the pools were allowed to dry out fully between watering because saltcedar does not grow as well in constantly saturated conditions. Twenty first-instar larvae (one or two days post-hatching) were placed into nylon sleeves (0.4 mm mesh size) during the last week of August 2004. This experiment was terminated on the date when pre-pupal development was first observed, and all larvae were then collected, dried and weighed and mean larval biomass per replicate plant was used to analyze data with one-way ANOVA.

Larvae grew and developed to the pre-pupal stage on all *Tamarix* genotypes, indicating that successful development was physiologically possible on each. In the greenhouse study, although average survival was moderately low (mean survival =

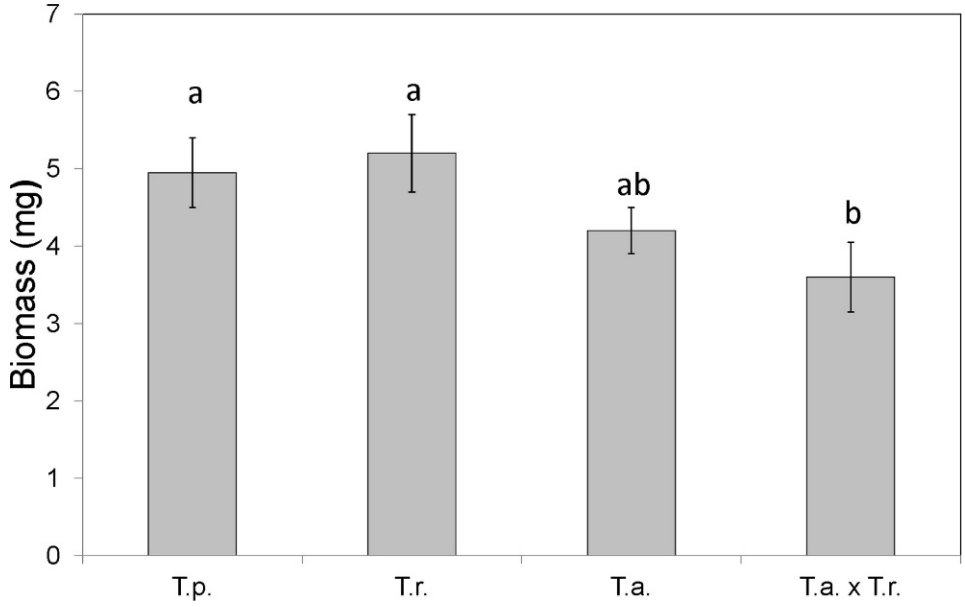

Figure 2. Larval biomass on the first day pupal development was observed (+ 1 SE) on different genotypes of *Tamarix* spp.; T.p. = *T. parviflora*, T.r. = *T. ramosissima*, T.a. = *T. aphylla*, T.a. X T.r. = hybrid of *T. aphylla* and *T. ramosissima.* Matched letters indicate non-significantly different pairs.

34%) owing to artifacts related to the experimental set-up but unrelated to treatment, final biomass of surviving larvae did not differ significantly among treatments (Table 1). Mean pre-pupal dry biomass was 4.54 mg (0.21 SE); salt addition may have led to lower biomass, [4.37 (0.23 SE) vs. 4.71 (0.14 SE) mg] but this trend was not statistically significant. Growth rate was, however, significantly affected by two treatment factors, nutrient addition and host species, as expressed by days to reach the pre-pupal stage (Table 1). Larvae achieved the pre-pupal stage approximately 3 days earlier in treatments enriched with nitrate, and as an aggregate they developed to this point on *T. ramosissima* 1.2 days faster than on *T. parviflora*. These data suggest that better quality resources lead to increased growth rate and accelerated development to the reproductive stage. *T. ramosissima* appears to be a moderately superior resource, but nutrient enrichment can compensate for the apparent poorer food quality of *T. parviflora*. The apparent tendency for salt addition to increase growth is a curious result that is hard to explain, unless it may be associated with enhanced feeding behavior on a host that typically has high tissue salt content.

In the outdoor container experiments *Tamarix* genotype was significantly related to larval biomass ($P < 0.01$) (Fig. 2). There was no statistical difference in growth, however, between the two *Tamarix* species of primary interest, nor between them and pure *T. aphylla* despite a strong trend toward the latter species being a poorer food source. Interestingly, the hybrid of *T. aphylla* × *ramosissima* yielded significantly lower insect growth than the original *T. ramosissima* source (Tukey pairwise test, $P = 0.014$).

Thus, *D. carinulata* can grow to maturity on all these host taxa even if growth rate or reproductive output may be slightly retarded by low nutrient conditions or by

feeding on *T. parviflora* or genetic forms of *T. aphylla* instead of the superior *T. ramosissima*. But the primary conclusion of container plant feeding experiments is that, as long as insects are able to colonize the various forms of *Tamarix*, these hosts appear to be satisfactory for successful development.

Study 3—Field Host Plant Choice Experiment

Plants were cultivated at the Humboldt River, Nevada field site in this study, using cuttings collected on-site (*T. ramosissima*) and from Cache Creek, Yolo County, California (*T. parviflora*). The latter species occurs adventively in parts of the western Great Basin, and its growth was robust when planted at this site, as was that of the locally-collected species. Plants were transplanted in June of 2003, forming 20 blocks in two rows, each consisting of two plants of each type to form a quad 1 meter square in a shallow depression to hold water. Irrigation was from a 5000-gallon water truck parked nearby, and a timer allowed gravity-fed water to flow through plastic irrigation line for two hours (approx. 25 liters) every four days for the first season. Site conditions are more fully described by Dudley & Kazmer (2005).

This setup was designed for testing the influences of, and interactions between, *D. carinulata* and the leafhopper, *Opsius stactogalus*, which involved placing screen cages over all plants except for no-cage control treatments. Results of that experiment will be reported elsewhere, but two sets of observations provided information related to acceptability of these two host types for the beetles. The first was before herbivore treatments were initiated and soon after cages were installed in June 2003. These plants were located near the area where *D. carinulata* had established in the open in 2002, while in 2003 population growth exceeded our expectations. The subsequent complete defoliation of existing *T. ramosissima* trees adjacent to the planting site by extremely high densities of *Diorhabda* larvae resulted in dispersal of larvae in search of alternative foods (Dudley & Kazmer 2005). The experimental plantings were two to 10 m away from the defoliated trees, and the mesh size of the cage screen was large enough (1.2 mm) to expose plants of both *Tamarix* genotypes to dispersing early instar larvae.

The second set of observations was in 2004, after this herbivore manipulation experiment was terminated and cages were removed, making plants accessible to *D. carinulata* adults as well as larvae. Nearly all plants in the 'control' treatment (caged, no herbivores) were growing vigorously and were sufficiently established that supplemental watering was no longer needed. We focused our attention on these "control" plants because they were largely unexposed to beetle feeding (some interlopers were manually removed during the course of the herbivory experiment). They were large enough at this time (size was variable, but did not differ between species) that branches of plants in each quad were often touching, meaning that movement of insects between plant species was possible without leaving the plant. For both sets of observations, herbivore impacts were assessed by digital photography, placing a large placard with a 1.3 m rule drawn onto it behind each plant so that a two-dimensional plant "area" could be evaluated in the resulting images. Quantification was by placing a grid over the on-screen images, adjusted to standardize size, and counting the number of cells occupied by green vs. defoliated tissue. "Defoliation" was the proportion of defoliated area to total foliar area in this two-dimensional representation.

In the 2003 observations, dispersing larvae encountered the experimental plantings before exclusion cages were fully secured, and those plants in the row adjacent to the

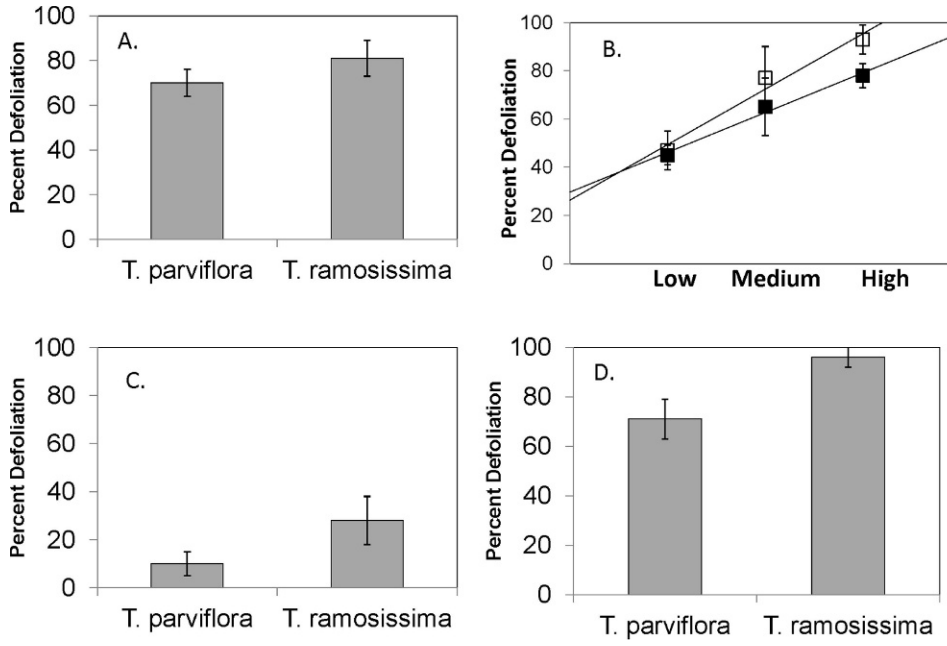

Figure 3. Impact of *D. carinulata* to *T. ramosissima* and *T. parviflora* grown and colonized under field conditions. (A) Defoliation in 2003 experimental cages. (B) Defoliation in relation to herbivore abundance categories in 2003 (*T. parviflora* = ■, *T. ramosissima* = □). (C) Early season 2004 defoliation. (D) Defoliation three weeks later than in C.

defoliated vegetation were more heavily colonized than the second row. Thus, a gradient of herbivory was apparent, and insects were counted on each plant and grouped into three abundance categories for regression against percent defoliation of that plant. Categories of abundance are reported rather than actual numbers, since insect censuses at sampling time do not accurately reflect numbers during the course of defoliation. Both *Tamarix* species experienced moderate but similar defoliation ($P > 0.10$, *t*-test), approximately 70% overall for *T. parviflora* and 80% for *T. ramosissima* (Fig. 3A). There was a clear overall relationship of herbivory to insect abundance ($r^2 = 0.40$, $P < 0.01$), but the slope of the relationship for each species appears only slightly greater for *T. ramosissima* compared with its congener (Fig. 3B); slopes were not compared statistically.

In 2004, early season defoliation of *T. ramosissima* was greater than that of *T. parviflora* by a factor of three, reflecting an apparent preference by adult beetles for oviposition on *T. ramosissima* (Fig 3C). Because herbivore abundance on nearby plants was relatively low compared with the epidemic levels occurring the year before, there were few larvae dispersing to experimental plants. Three weeks later all *T. ramosissima* plants were almost completely defoliated by maturing larvae, whereas *T. parviflora* still retained substantial live foliar tissue (Fig. 3D). Percent defoliation was significantly greater for *T. ramossisima* on both dates (*t*-test, $P < 0.01$), and this pattern was maintained over the course of the season as *D. carinulata* abundances declined in the general area, although some re-growth of both plant species did occur. Of the 10 *T. ramosissima* plants used for these observations, five

appeared to be dead by the end of the season, whereas only two *T. parviflora* suffered mortality; no plants recorded as 'dead' indicated any recovery the following year.

Study 4—Natural Dispersal and Host Choice

Because *T. parviflora* can be found within the range of *T. ramosissima*, albeit at lower frequencies, this gave us the opportunity to document colonization and impact of naturally dispersing *D. carinulata* adults under open field conditions. One such site was on the lower reaches of Walker River (Mineral Co., Nevada) where three small stands of *T. parviflora* were present amongst the approx. 2000 ha of *T. ramosissima* dominated floodplain. One stand was comprised of four 0.5 km long rows of large trees planted several decades ago, with the nearest *T. ramossisima* approximately 50 m distant. Another consisted of plants that established in several rows by natural seeding (presumably from the upstream planted stock) along old shores of Walker Lake as it receded, and these plants were often within 20 or fewer meters of *T. ramosissima* plants. The third stand was a small number of isolated trees roughly equidistant between the other two locations, but several hundred meters away from the river channel and amongst moderate-density stands of *T. ramosissima*. Finally, somewhat fewer than 100 tamarisk plants, with roughly equal numbers of each species, were present approximately 50 km south of the Walker River sites in and around the town of Mina, Nevada. These were of various sizes and aggregated loosely into several groups of plants, each consisting primarily of one species or the other.

During the period from late summer 2004 to mid-summer 2005 *D. carinulata* adults dispersed southward into the *T. parviflora* sites from the original research release area along the Walker River. Insect numbers were periodically monitored by censusing larvae and adults on representative 40 cm long branches of each target tree, along with damage estimated as percent of the plant volume defoliated. Foliage was also swept with a standard entomological sweep net on some dates, particularly when insect numbers were low. At least 5 trees, and usually 8 to 40, were sampled on each date.

The large "planted" stand of *T. parviflora* trees was within the zone of 2004 adult dispersal from the original release zone, and in September nearby *T. ramosissima* plants to the north (toward source of dispersal) and south (away from the direction of dispersal) experienced defoliation rates of 10 to 80% while almost no insects were present on the *T. parviflora* plants in between (< 3 *D. carinulata* adults per five-sweep sample vs. >250 adults and larvae on *T. ramosissima*; minimum 5 samples from each host species). The following year *D. carinulata* was again more abundant on *T. ramosissima* than on *T. parviflora* (Fig. 4), with the exception of early May when adults were emerging from over-wintering in the litter. They were initially only found on *T. parviflora* which was already flowering (but no eggs or larvae were present) and ignored *T. ramosissima*, which had not yet produced flowers nor substantial foliage. By early summer this situation had reversed, with small numbers of adults and larvae collected from *T. parviflora* and only trivial defoliation (Fig. 4). The nearby *T. ramosissima* were largely defoliated yet adults and larvae remained in greater abundance throughout the season (Fig. 4). Larval dispersal resulted from *T. ramosissima* over-exploitation, and larvae were noted on the ground moving away from these plants, but the distance away from the *T. parviflora* stand presumably limited their colonization because few larvae were ever seen on *T. parviflora* at this site.

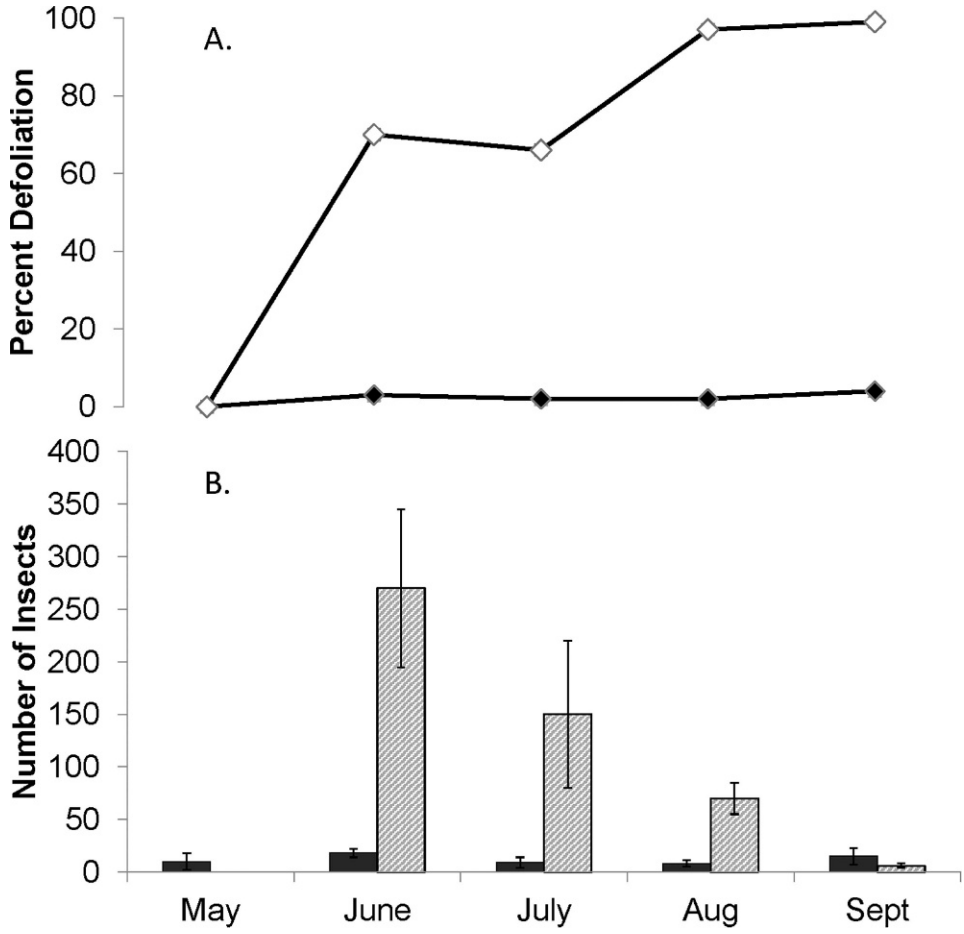

Figure 4. *Diorhabda carinulata* abundance and corresponding defoliation of each host species over the course of a season at the Walker River, NV field site. (A). Number of larvae and adult insects (± 1 SE) per 40 cm branch ($n \geq 5$ branches; *T. parviflora*, = ●, *T. ramosissima* = ○) on sampling dates (single date in May and September, mean of 2 dates in other months). (B). Corresponding proportion of host plants defoliated. Solid bars represent *T. parviflora* and cross-hatched bars represent *T. ramossisima*.

The naturally established *T. parviflora* patch was exposed to adult colonization early in the 2005 season, and initially was relatively untouched on 18 June with 13.4 (± 12.3 SD) adult *D. carinulata* collected per five-sweep sample ($n = 8$ samples) while the nearby *T. ramosissima* were more heavily colonized by 162 (± 104 SD) adults and 105 (± 35 SD) early instar larvae per sweep sample; little defoliation had occurred by this date. Three weeks later (8 July) numbers were similar but impact was dramatically different [*T. parviflora*: 14 (± 12 SD) adults and 38 (± 16 SD) most first and second instars; 1% defoliation; *T. ramosissima*: 62 (± 20 SD) adults and 94 (± 43 SD) larvae, mostly third instars; 65% defoliation]. A colleague using a different sampling method (sticky trap cards hung in trees) found that adult beetles were twice as common in *T. ramosissima* than in the less preferred species (H. Thomas, unpublished data).

By 11 August, however, insect numbers had declined on both host plants with a mean of 8 late instar larvae on *T. parviflora* but more than 40 larvae per sweep

Figure 5. Adjacent trees in mid-summer at Walker River, NV study area showing difference in defoliation based on host species. Tree on left is *T. ramosissima* and tree on right is *T. parviflora*. Both plants are ca. 4 m in height.

sample on *T. ramosissima*, while numbers were roughly reversed a few weeks later (22 September) with a mean of 16 insects (larvae and adults) on *T. parviflora* and 6 on *T. ramosissima*. Colonization of *T. parviflora* was sufficient to cause defoliation rates of 45% (range 15–65%) on this *T. parviflora* patch, whereas *T. ramosissima* was, on average, 98% defoliated and no longer supported the insects. Similar results were observed the following year, *T. ramosissima* experiencing >99% defoliation of all plants in July 2006 (two dates), while most *T. parviflora* retained 80 to 90% live green foliage although some individual plants were approximately 90% defoliated, presumably by insects dispersing from fully defoliated plants.

The individual trees at the intermediate location provided dramatic visual evidence of differences in host suitability to adult *D. carinulata* (Fig. 5). The scattered *T. ramosissima* trees nearby were heavily attacked but the total insect population here was apparently not large enough to result in substantial larval dispersal and even by the end of the season *T. parviflora* showed less than 10% defoliation.

Finally, colonization of the Mina mixed *Tamarix* spp. stands occurred late in the 2005 season, involving long distance dispersal when insect populations achieved epidemic levels in the main tamarisk infestations on the lower Walker River. Dispersal was documented through the use of pheromone traps, and required crossing of gaps lacking tamarisk of over 10 km (E. Andress unpublished data). By 2 September 2005 adult densities on *T. ramosissima* were 21.8 insects per sweep sample ($n = 6$), causing defoliation in the range of 60 to 95%. No significant defoliation of *T. parviflora* was observed at this location, and only 2.4 adult insects were collected per sweep sample ($n = 4$). September is generally too late for reproduction (Bean et al. 2007), so establishment on this host species would not occur. Population sizes are unlikely to be large at this site because of the small number of host plants available. In fact, in 2006 *T. parviflora* was virtually untouched at the Mina site while moderate numbers of insects were on *T. ramosissima*, which in June showed a mean of 39% defoliation and only three individual plants experienced near-total defoliation by herbivores. Because insect abundances decline in years following initial, epidemic establishment and dispersal (T. Dudley unpublished data), it is unlikely that *T.*

parviflora in the Walker River and Lake region will experience future colonization by *D. carinulata* sufficient to inflict significant damage.

Discussion

Establishment Failure with Tamarix parviflora. *Tamarix parviflora* is formally designated as a target for biological control (Richard 2003), but cage and field introductions to-date, particularly using the central Asian form of *D.* '*elongata*' (= *D. carinulata*) have generally failed (Dudley et al. 2006) despite success against the more abundant *T. ramosissima* and its genetic variants (DeLoach et al. 2004). The combination of experiments and field observations described here provides explanation for the establishment failures with this host species. The beetle is clearly able to feed and develop on *T. parviflora* so it is within the agent's physiological host range, even if slightly poorer performance was observed. Larvae do not appear to distinguish between the two host taxa, as those dispersing from *T. ramosissima* (or its hybrid forms) routinely colonized *T. parviflora* if it was accessible (see also Moran et al. 2009). Other larval insect stages, e.g., *Helicoverpa armigera* Hübner, 1805 (Noctuidae) (Rajapakse & Walter 2007), can distinguish and show preferences among different but suitable hosts, and the preferences are borne out in growth-related differences, but this ability does not appear to be important with *Diorhabda,* at least with the *D. carinulata* species evaluated here. Host-range testing in quarantine prior to and following field release has routinely shown acceptability across *Tamarix* species but often with moderately lower utilization of some forms (Milbrath & DeLoach 2006b, Tracy & Robbins 2009).

Host Choice by Adult Beetles. Adult avoidance of *T. parviflora* appears to be a primary determinant of establishment failure where it is the target species. *D. carinulata* is responsive to airborne chemical cues such as male-derived aggregation pheromones and volatile plant compounds (Cosse et al. 2005, 2006). The only instance in which the insects appeared to show an opposite host "preference" was early in the season at our Walker River site when *T. parviflora*, which flowers prior to fully leafing out, was in full bloom before substantial foliage production had occurred on adjacent stands of *T. ramosissima*. The *Diorhabda* behavioral response to plant volatile compounds is less specific than that to pheromones (Cosse et al. 2006), so odors emanating from *T. parviflora* flowers could have provided a feeding stimulus attracting adult insects. These insects were just emerging from over-wintering, their nutritional reserves having been depleted during approximately 6-month diapause and quiescence, so food acquisition is likely to precede response to reproductive stimuli (pheromones) (Lewis et al. 2003).

We have also observed in three cases, twice in Nevada (T. Dudley unpublished data) and at the Wyoming site (D. Kazmer, personal communication), that *T. ramosissima* plants defoliated in one year were initially avoided by adults emerging from winter diapause the following spring. "Avoidance" may have resulted from a weaker or delayed plant chemical signal compared with nearby plants that had never been attacked, or possibly an induced chemical defense. These behaviors suggest that host plant choice is determined by adult attraction to plant odors (or other traits) rather than inability of larvae or adults to develop on some *Tamarix* species. Foliage of *T. parviflora* has, indeed, been used routinely for continuous rearing of *Diorhabda* spp. in the laboratory, particularly *D. carinulata* (Bean et al. 2007). The differences in performance on different species or forms of *Tamarix*, whether measured as larval

survival or adult egg production, are significant (DeLoach et al. 2004, Tracy & Robbins 2009) but insufficient to account for inability of *D. carinulata* to establish on *T. parviflora*. Herbivorous insects commonly use chemical cues that identify plant substrates as suitable for oviposition (Dethier 1982), and rejection of otherwise suitable substrates may occur because they are not recognized as a host plant (Mayhew 1997). Theoretically, insects may adapt over many generations to use a physiologically acceptable, but non-attractive host (Thompson 1998) but in the timeframe of a biocontrol development program, such a ''switch'' is not feasible.

Other Factors Potentially Inhibiting Establishment. Establishment failures of *D. carinulata* can be the consequence of other factors, including developmental mismatches with photoperiod, local environmental conditions that limit survival, and predation (Lewis et al. 2003, DeLoach et al. 2004). The photoperiod mechanism is related to the physiological response of the Fukang ecotype of *D. carinulata* to light such that as daylength decreases to about 14.5 h, reproductive diapause is induced (DeLoach et al. 2004, Bean et al. 2007). This beetle ecotype originates at approximately 44°N in NW China, and has an increasingly attenuated reproductive period with decreasing latitude. Below a latitude of approximately 38° N, this cue can arrive too soon to allow successful over-wintering because temperatures are still warm, and the over-wintering adults simply lack the metabolic capacity to survive until the following spring (although we have documented selection for delayed diapause induction that may facilitate future establishment further south; see Bean et al. 2012). Developmental asynchrony was the explanation for only a single cohort being produced (Fig. 1), and contributed to establishment failure from low over-winter survival, at the Owens Valley *T. ramosissima* site (37.1° N). The San Antonio Creek site is at a latitude of about 35.9° N, too far south for establishment of this biocontrol agent; however, the other two *T. parviflora* locations are north of 38° (Cache Creek at 38.7°, Bear Creek at 39.0°). Sites in northern Nevada, Utah, Colorado and Wyoming with similar latitudes but where *T. ramosissima* is the target species produced much better population growth in field cages and in the open (DeLoach et al. 2004). Thus daylength, or latitude, is unlikely to be an important factor limiting establishment west of the Sierra Nevada.

Successful release sites have been quite variable in environmental conditions, from mesic lakeshores and perennial streamsides to alkaline sinks and dry terraces (DeLoach et al. 2003), and source locations in central Asia are likewise both diverse and physiologically stressful (Kovalev 1995, Li et al. 2000). Summer climates are roughly similar at nearly all release sites, with high temperatures (average monthly maxima within 3°C), and low precipitation and humidity. While winter temperatures are substantially warmer at *T. parviflora*-infested sites in California than at interior *T. ramosissima* sites, weak population growth and establishment failure resulted well before the onset of winter. Climate matching models suggest that most *T. parviflora* locations are within the region considered suitable for survival of the Chinese ecotypes of the *D.* '*elongata*' species group (Tracy & Robbins 2009). Thus, it is unlikely that autecological factors are important in explaining failures at these sites. Inundation, whether related to high water from snowmelt and other runoff or from reservoir management, could be highly detrimental to *Diorhabda* spp. which pupate and over-winter at the interface between the soil and litter layers (Lewis et al. 2003). Abnormally high water during 2006 did result in population decline at the Humboldt River sites (T. Dudley,

unpublished data), but original field testing of *D. carinulata* was during a sustained drought and no inundation occurred during this period.

Predation is an important factor at nearly all release sites in North America (as well as in the Eurasian range) (Tracy & Robbins 2009), and is likely the explanation for cage success but open release failures at the eastern California, Idaho and the Oregon sites, and possibly others (Herrera 2003, DeLoach et al. 2004, Dudley & DeLoach 2004, D. Kazmer personal communication, J. Milan personal communication). Inside the cages we typically place ant baits to reduce this impact. Important ant predators at interior sites belong to the genera *Formica* Linnaeus, 1758 and *Pogonomyrmex* Mayr, 1868, which were uncommon at the *T. parviflora* sites (although the introduced Argentine ant, *Linepithema humile* Mayr, 1868, was a nuisance intruder at the Cache Creek site). A variety of other predatory arthropods are widely distributed (Strudley & Dalin, in press), but are certainly no more common at these sites than at most of the successful *T. ramosissima* sites. Host plant unacceptability to adult insects remains as the only reasonable explanation for the establishment patterns observed.

Larval Growth Response to Host Species and Quality. Significant, albeit minor growth differences are probably related to chemistry of *Tamarix* foliage, a genus known for its complex chemical composition that presumably drives the high degree of specificity by many herbivores while largely excluding generalist consumers (Kovalev 1995). Tamarisk is a commercial source of tannins in some regions (Heneidy & Bidak 2004), but there is limited information on comparative chemical differences among taxa (Parmar et al. 1994, Bikbulatova & Korulkina 2001). Some tannin compounds inhibit insect growth by binding proteins and reducing digestibility (Bernays 1989), so higher concentrations among plant taxa, particularly of gallotannins (Quideau et al. 1995), could potentially be a cause of reduced utilization. However, gas chromatography analysis of foliar gallotannin concentrations showed no significant difference between *T. ramosissima* and *T. parviflora* grown under common garden field conditions (T. Dudley, unpublished data). Differences in phenolic compounds also can reduce food quality for herbivores, either among plant taxa or in response to feeding damage (inducible defenses) (Agrawal 1998). In another experiment, we observed growth differences in *D. carinulata* larvae feeding on regrowth foliage from previously defoliated *T. ramosissima* compared to undefoliated plants (3.2 vs. 3.8 mg on container grown plants), suggesting an induced defensive chemical response to herbivory; however, we observed no clear pattern in concentrations of 32 constituent phenolic compounds from plant types, so growth differences appear unrelated to secondary defensive chemicals in this case (A. Caires, unpublished data).

Nitrogen enrichment lead to increased larval growth response by *D. carinulata*. Interestingly, enhanced growth rates did not lead to larger adults, but instead to earlier pupation at similar pre-pupal biomass. In a similar experiment not included here, N-augmentation to *T. parviflora* again increased larval growth rate, but resulted in significantly smaller, not larger, pre-pupal biomass (4.1 vs. 4.8 mg, $P < 0.001$). Higher food quality (tissue N concentration) is well-known to increase herbivore growth, typically resulting in larger individuals (Mattson 1980). Accelerated development at the expense of larger adult size could be interpreted as a mechanism for an indeterminate multi-voltine species, which *Diorhabda* species appear to be (Li et al. 2000, Dalin et al. 2010) to increase reproductive fitness under

favorable conditions through production of an additional cohort (Nylin & Gotthard 1998). Because diapause timing is relatively inflexible but is only an adult response (Bean et al. 2007), *D. carinulata* may benefit from the capacity for rapid larval growth and development to the adult stage to produce adults ready to enter winter diapause. We assume that nutrient augmentation under field conditions may enhance population increase and target impact of this biocontrol agent; nonetheless, nutritional quality probably plays only a minor, if any, role in explaining differences in insect response to *Tamarix* species in the field.

Host Specialization and Saltcedar Biocontrol. Contrary to concerns that *Tamarix* biological control agents may damage related non-target plants, our results indicate that *D. carinulata* (the *Diorhabda* species most widely released for *Tamarix* biocontrol in North America) is largely restricted to one (*T.* '*ramossisima*', including *T. chinensis* and hybrid forms) of its two intended hosts, and that within the *Tamarix* genus some species are largely immune to substantial damage under field conditions. Herbivore specialization at the intra-generic level is common, as indicated in other weed biocontrol programs using Coleoptera [e.g., the weevil *Euhrychiopsis lecontei* Dietz, 1896 on Eurasian water milfoil (*Myriophyllum spicatum*, Haloragaceae) (Sheldon and Creed 2003); various insects on weeds in the genus *Solanum* (Solanaceae) (Olckers 2002); *Aphthona* spp. flea beetles on leafy spurge (*Euphorbia esula*) (Gassmann 1996); or, the leaf beetle *Galerucella* spp. on purple loosestrife (*Lythrum salicaria*) (Blossey et al. 2001)]. We are increasingly confident that this degree of specialization within the *Tamarix* genus indicates that risks are minor or probably non-existent for other plants that can sustain *Diorhabda* development, but which are relatively unattractive to insects seeking host plants for oviposition [e.g., *T. aphylla* used horticulturally across much of the southwestern U.S. and northern Mexico (Milbraeth & DeLoach 2006a, Moran et al. 2009) and *Frankenia* spp., low-growing halophytic sub-shrubs that occasionally co-occur with *Tamarix* spp. (Lewis et al. 2003, Dudley & Kazmer 2005, Milbrath & DeLoach 2006b, Herr et al. 2009).

On the other hand, the *T. aphylla* × *ramosissima* hybrid offers conflicting evidence of likelihood of attack. Larval growth on it was slightly lower than on *T. ramosissima*, suggesting that the hybrid form may be somewhat less susceptible to biocontrol, while in another study this hybrid was more attractive for oviposition than were pure *T. aphylla* plants and statistically equal to the *T. ramosissima* experimental hosts (Moran et al. 2009). We anticipate that field populations of *T. aphylla* hybrids with saltcedar (*T. aphylla* × *ramossisima*, *T. aphylla* × *chinensis*), occasionally found in the lower Colorado River region and some other southwestern locations (Gaskin & Shafroth 2005), should experience substantial damage when *Diorhabda* eventually enters these ecosystems. These are already targets for eradication by National Park Service weed managers (C. Deuser, personal communication).

In the case of *T. parviflora*, however, this non-preferred host is one of the two named saltcedar targets for biocontrol (DeLoach et al. 1996, Richard 2003), indicating that further research may be needed to develop agents that are effective against this weed. The taxon we were working with, *D. carinulata*, is from central Asia and is not sympatric with *T. parviflora* in its eastern Mediterranean/western Asia distribution (Baum 1978, Kovalev 1995, Tracy & Robbins 2009) so it may not be surprising that this saltcedar species is not recognized by the insect as a suitable host. Several other species of *Diorhabda* have been tested or released in North

America to extend saltcedar control to locations where *D. carinulata* has not been effective (Tracy & Robbins 2009, Bean et al. 2007). One of these (*D. elongata*), from the Mediterranean region at 35.2° N, seems to perform somewhat better following inundative releases over the course of 2 + years onto *T. parviflora* at one of our California sites (Cache Creek) (Thomas et al. 2010). Population expansion has not been extensive, nor have transfers to new locations proven successful, and it remains too early to conclude that successful establishment and control have occurred on this host. Both this beetle species and another, *D. carinata* from southwestern Asia, were shown in choice experiments to recognize *T. parviflora* as an oviposition host (Dalin et al. 2009) suggesting that potential exists for suppressing this biocontrol target.

From a management perspective, *T. parviflora* lacks the qualities of a high priority biocontrol target. Unlike other saltcedars that can produce seed over much of the growth season, *T. parviflora* only flowers for a limited period in spring. Because *Tamarix* seeds are only viable for a few days (Young et al. 2004), and seed set of *T. parviflora* appears to be low relative to *T. ramosissima* (K. Heckman & T. Dudley, unpublished data), its potential for germination and establishment is much lower than that of the more widespread and prolific genetic forms of saltcedar. Few *T. parviflora* infestations achieve the areal cover of *T. ramosissima* and related forms (Dudley & Collins 1995, Gaskin & Schaal 2003), so the potential benefits of biocontrol relative to costs of developing agents may not be justified and resources may be better spent applying traditional chemical and mechanical treatments.

Where damage to *T. parviflora* by *D. carinulata* was significant owing to short-distance larval dispersal from defoliated *T. ramossisima* plants, an anomalous situation was observed suggesting a possible undesirable effect of biocontrol. Damaged saltcedar plants often will produce atypical late-season foliar growth and flowering, a response known from other plants that compensate for damage or stress via extended productivity (Hendrix 1990). At the Walker River, partially defoliated *T. parviflora* produced flowers in late August and September, well past their normal flowering period of May to early June, at the same time as water levels were receding following unusually high snowmelt runoff. Germination was extensive under these conditions, representing the only germination we have observed by this species during our studies in the region.

In fact, the selectivity for *T. ramosissima* (sensu lato) over *T. parviflora* by *D. carinulata* may be a positive trait for implementation of the saltcedar biocontrol program. Ornamental saltcedars are planted throughout the western states for landscaping purposes, and *T. parviflora* is often used for this purpose (Gaskin & Kazmer 2006, T. Dudley, personal observations). It may be that the horticultural value of this form outweighs the impacts of its limited invasion, and avoidance mitigates the need to protect landscape plants from herbivory by applying insecticides. At the time of inception of the saltcedar biocontrol program, the distributions and identities of *Tamarix* species and genotypes across North America were poorly known (Baum 1978, Gaskin & Schaal 2003), so it was difficult for researchers to appropriately target agents against specific genetic forms of the weed. Our research indicates that this agent is highly selective, allowing targeted implementation against some forms of *Tamarix* and bypassing those less-damaging forms of the weed.

More generally, these results provide support for the contention that the risk of damage from introduced biocontrol agents to non-target plants, while real, may be a

lesser concern than is often surmised. Caution is appropriate when anticipating host ranges of biocontrol agents released into open field circumstances (McEvoy 1996); however, accumulating evidence shows that rarely if ever do specialist herbivores introduced against pest plants expand their host ranges to taxa not predicted in, or predictable from lab testing (Willis et al. 2003, Clement et al. 2009). In fact, it may be typical that the actual host range is more restricted than that observed under laboratory conditions (Pratt et al. 2009). Lab and field cage host preference and performance results do not always predict open field host ranges in weed biological control (Louda et al. 2003) owing to behavioral artifacts of herbivores in confined tests (Heard 2000), and because climate, host quality, competition and predation can all influence the field host ranges of weed biocontrol agents (Culliney 2005, Sheppard et al. 2005). Yet, as long as questions remain regarding potential to utilize non-target as well as target hosts, post-release monitoring remains an important objective for improving our assessment of non-target impacts (van Driesche et al. 2010).

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