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Research article

Hitching a ride: Seed accrual rates on different types of vehicles

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ABSTRACT

Human activities, from resource extraction to recreation, are increasing global connectivity, especially to less-disturbed and previously inaccessible places. Such activities necessitate road networks and vehicles. Vehicles can transport reproductive plant propagules long distances, thereby increasing the risk of invasive plant species transport and dispersal. Subsequent invasions by less desirable species have significant implications for the future of threatened species and habitats. The goal of this study was to understand vehicle seed accrual by different vehicle types and under different driving conditions, and to evaluate different mitigation strategies. Using studies and experiments at four sites in the western USA we addressed three questions: How many seeds and species accumulate and are transported on vehicles? Does this differ with vehicle type, driving surface, surface conditions, and season? What is our ability to mitigate seed dispersal risk by cleaning vehicles? Our results demonstrated that vehicles accrue plant propagules, and driving surface, surface conditions, and season affect the rate of accrual: on- and off-trail summer seed accrual on all-terrain vehicles was 13 and 3508 seeds km^{-1}, respectively, and was higher in the fall than in the summer. Early season seed accrual on 4-wheel drive vehicles averaged 7 and 36 seeds km^{-1} on paved and unpaved roads respectively, under dry conditions. Furthermore, seed accrual on unpaved roads differed by vehicle type, with tracked vehicles accruing more than small and large 4-wheel drives; and small 4-wheel drives more than large. Rates were dramatically increased under wet surface conditions. Vehicles indiscriminately accrue a wide diversity of seeds (different life histories, forms and seed lengths); total richness, richness of annuals, biennials, forbs and shrubs, and seed length didn't differ among vehicle types, or additional seed bank samples. Our evaluation of portable vehicle wash units showed that approximately 80% of soil and seed was removed from dirty vehicles. This suggests that interception programs to reduce vehicular seed transportation risk are feasible and should be developed for areas of high conservation value, or where the spread of invasive species is of special concern.

1. Introduction

The role that humans play in the introduction and subsequent dispersal of native and non-native species has recently garnered attention (Arevalo et al., 2005; Pauchard et al., 2009; Seipel et al., 2012). Plant communities along transportation corridors can differ significantly from the composition of adjacent interior communities (Gelbard and Belnap, 2003; Tikka et al., 2001; Veldman and Putz, 2010). The effects of road maintenance (mowing, herbicide spraying, and grading of unpaved roads), combined with the abiotic effects of roads (altered substrate and hydrology), make roadsides unique ecosystems that can be more susceptible to the establishment of ruderal and non-native vegetation when compared with interior ecosystems (Coffin, 2007; Greenberg et al., 1997; Hansen and Clevenger, 2005; Hendrickson et al., 2005; Pickering and Mount, 2010; Rauschert et al., 2017; Veldman and Putz, 2010; Zwaenepoel et al., 2006).

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In addition to disturbances that create conditions favorable for the establishment of undesirable plant species, transportation corridors and roadways can act as vectors for seed transport (Taylor et al., 2012; Veldman and Putz, 2010; Vakhlamova et al., 2016; von der Lippe and Kowarik, 2007). Studies have recorded the presence of seeds from a range of species on and in vehicles (Auffret and Cousins, 2013; Clifford, 1959; Hodkinson and Thompson, 1997; Lonsdale and Lane, 1994; Pickering and Mount, 2010; Schmidt, 1989; Veldman and Putz, 2010; Zwaenepoel et al., 2006). Using roadway tunnels to study seed transport by vehicles, von der Lippe and Kowarik (2007) found significant seed quantities in tunnels and concluded that long-distance transport of seeds by vehicles is the rule rather than the exception. Seed transport by vehicles is likely due to both the slip stream (airflow) around a vehicle as it moves (von der Lippe et al., 2013) and/or by physical attachment onto the vehicle's frame (Taylor et al., 2012).

Seed transport by vehicles is likely to disperse seeds farther than other anthropogenic modes such has hiking (Wichmann et al., 2009) or mountain biking (Weiss et al., 2016). Taylor et al. (2012) showed that >85% of seeds previously attached to a vehicle remained in place for several hundred kilometers under dry conditions on either paved or unpaved roads. In their roadway tunnel study, von der Lippe and Kowarik (2007) found that non-native seeds accounted for half of the number of species found and over half of the total number of seeds. Furthermore, Vakhlamova et al. (2016) found national roads, where vehicles likely travel longer distance and into new regions, have higher richness and percentage of non-native species than local roads. Roadways have been found to contribute to the spread of non-native species in many different systems: mountain landscapes (e.g. Arevalo et al., 2005; Pauchard et al., 2009; Seipel et al., 2012), semi-arid landscapes (Gelbard and Belnap, 2003), taiga (Hendrickson et al., 2005), temperate deciduous forests (Huebner, 2010), and tropical dry forests (Veldman and Putz, 2010). The construction of new roads, and maintenance of existing ones, coupled with the increased vehicular traffic (on- and off-road), presents a unique conservation challenge in terms of preventing and managing the spread of non-native and invasive plant species.

Despite the literature on seed dispersal by vehicles and differences in the vegetation alongside and adjacent to roadways, studies have not quantified the rate of seed accumulation by different vehicle types, under different driving conditions (i.e. wet or dry conditions), or along different surfaces (paved, unpaved and off-road). This information is necessary to determine the potential of vehicular traffic to act as seed dispersal vectors, and assess the risk of spread of plant species (Auffret and Cousins, 2013). Thus, the first goal of the study was to evaluate the rate of seed accrual onto vehicles under a range of different conditions. For this goal, our objectives were to evaluate the rate of seed accrual (1 or 100 km^{-1}), total seed abundance, and species richness on: 1) all-terrain vehicles driven on- or off-trail in two seasons; 2) four different vehicle types driven on different surfaces during early summer.

To address the potential for vehicles to act as seed dispersal vectors, the USA Forest Service currently commissions portable vehicle wash units (VWU) to clean vehicles at sites where wildfires are being actively managed, the military cleans vehicles between training activities, and there is interest in the use of portable wash units to treat vehicles entering sensitive areas. However, the effectiveness of current portable cleaning equipment has not been quantified and there are few established guidelines by government agencies. To address this need, the second goal of our study was to quantify the effectiveness of different portable vehicle wash units (VWU) at removing plant propagules and soil from different types of vehicles. The objectives for this second goal were: 1) evaluate the efficacy of five different VWUs to remove soil waste from different vehicle types, 2) determine the efficacy of the VWU washing protocol (cleaning, filtering, and containment) on the survival of different seed types, 3) quantify the efficacy of the primary VWU over different wash durations.

2. Methods

2.1. Seed accrual studies

Seed accrual was assessed in two ways: (1) using all-terrain vehicles (ATV) driven on- and off-trail in summer and fall; (2) using four vehicle types driven primarily on unpaved roads during early summer.

2.1.1. All-terrain vehicles driven on- or off-trail

Seed accrual onto recreational ATVs was assessed during the summer (July) and the fall (September) of 2008, in Montana, USA. All-terrain vehicles were driven a fixed distance (3.2 km) on two different courses, with different surfaces (on-trail and off-trail). Both courses ran through mixed sagebrush and open conifer habitat. The on-trail course was conducted on a 2.5 m wide unpaved former logging road (45° 26′ 13″ N, 111° 10′ 09″ S) and the off-trail course was nearby (45° 26′ 19″ N, 111° 14′ 03″ S). After travelling the set distance the ATVs were washed. Due to the VWU's filtering (200 microns) and containment procedures taking hours to complete, washes from multiple vehicle runs of the same type were collated for each replicate. There were three replicates on each of the two courses/surfaces, in each season. Before starting each replicate, the ATV was cleaned using the VWU. Following this pre-wash, the ATV drove a lap around the course, after which it washed and the seeds and soil it accrued during the lap were captured and contained by the VWU. This iteration occurred 24 times per replicate (total of 76.8 km). The vegetation was tall (~1 m) at the off-trail site, causing some seed to accumulate on the vehicle (e.g. on top of wheel fairings). These seeds were removed and bagged prior to washing, and the seed biomass weight was recorded by species. Germinable seed numbers were assessed by germinating them in the same manner as the vehicular seed and soil waste samples (see below). This provided consistent estimates between the different seed collection methods.

Once a replicate was completed, the soil and seed waste from the vehicles was contained and transported back to the Montana State University (MSU) Plant Growth Center, where it was mixed with pasteurized soil to provide a consistent medium, placed in seed trays, and monitored for growth. (In previous experiments, seedling survival of the pasteurization process and subsequent contamination of greenhouse experiments has been non-existent, thus we did not have control trays.) Seedling establishment from our trays was monitored and recorded for 20 months. Seedlings were removed from trays after they had been identified to the species level and the soil was subsequently disturbed to facilitate further germination. To address possible seed vernalization requirements, after 9 months and when new establishment had ceased, the trays were moved to a cold, dark room (4 °C) for 8 weeks. After the 8 weeks, the trays were returned to the greenhouse and new seedling emergence was monitored for another 9 months. Plants were grown under a 16-h photoperiod of natural sunlight supplemented with mercury vapor lamps (165 μE m−2 s−1) at 22 °C (day), with 15 °C at night. Plants were watered as needed throughout. A few plant specimens were grown to maturity for identification purposes, these were placed in separate pots and a different greenhouse, with the same climate conditions, to prevent any seed contamination of the seed trays. The process from containing the soil and seed waste in the field, through to recording individual species' abundance, is hereafter referred to as the VWU seed protocol.

2.1.2. Wheeled and tracked vehicles

Seed accrual was assessed on four vehicle types representative of vehicles operated by government agencies, private contractors, and the public: ATVs, 4-wheel drive Humvees (4WD), large extended wheel base 4WD (large 4WD), and tracked vehicles. These vehicles were driven on different surfaces (paved, unpaved, off-road) through sagebrush steppe vegetation; the primary surface was unpaved roads. To have access to different vehicle types and longer travel distances we collaborated with the Montana Army National Guard over three years (2007–2009) during their annual training exercises. Limestone Hills Training Area, Montana (46° 19′ 44″ N, 111° 33′ 56″ S) was the site of training exercises 1–2 and 4–5: June 10–13, 2007 (Exercise 1), June 18–20, 2007 (Exercise 2), June 12–14, 2009 (Exercise 4), and June 19–21, 2009 (Exercise 5). In 2008, the annual training exercise occurred at Orchard Training Area, Idaho (43° 17′ 04″ N, 116° 04′ 46″ S): June 1–12, 2008 (Exercise 3), USA. It should be noted that the timing of the exercises is before seed shed for the plant species of our sagebrush steppe sites and, as such, represents a conservative estimate of seed accrual.

Before each military training exercise, each vehicle was washed once using the military wash facilities and again with our primary VWU (Fig. 1 a, d). During each military exercise, the different types of vehicles were driven within the sagebrush steppe, as determined by the commanding officer; individual training exercises had to be flexible to mission changes in the field. The intent was to sample the same number of each vehicle type, driven the same route, for each training exercise. This did not occur due to vehicle attrition (e.g. breaking down, mission change). However, the exact route each vehicle travelled was recorded using a Global Positioning System (GPS) mounted on the vehicle. Therefore, after each training exercise, route data for each individual vehicle was downloaded and combined with digital site data to provide length driven on paved, unpaved, and off-road surfaces: most driving was performed on unpaved roads. Data were then summed by vehicle type and training exercise.

After each training exercise, vehicles of the same type were grouped and washed sequentially using the VWU. There was no set wash length, rather they were washed until visually clean and the duration of each wash was recorded (average of 6.5 min for ATVs and 4WD, 12 min for large 4WD, and 15.5 min for tracked vehicles under dry conditions; under wet conditions all wash times doubled). The soil waste obtained from each vehicle type wash was processed using the VWU seed protocol. The metrics obtained for each vehicle type and training exercise were: number of seeds accrued km^{-1} driven, total number of seeds accrued, and species richness. To evaluate species composition similarity between seeds accrued from the vehicles and site vegetation, we collected and germinated 21 soil seed bank samples from each site, along belt transects that ran perpendicular to unpaved roads. Each of the 21 soil samples consisted of 10 subsamples of 6 cm wide by 10 cm deep soil cores from within a 10 m^2 area. The samples were collected from the unpaved road and stratified away from the road edge: at 5 m and 50 m from the road edge at the Limestone Hills site, and 1 m and 5 m from the road edge at the Orchard Training site (farther away was not permitted).

2.2. Evaluation of vehicle wash unit studies

We performed a field experiment to quantify the effectiveness of five commercial portable VWU to clean soil waste from three different vehicle types (4WD, large 4WD, and tracked). This study was performed during the summer (July–August) of 2008, at the California Department of Forestry and Fire Prevention Training Facility (CalFire) in Ione, California (38° 21′ 55″ N, 120° 56′ 24″ S), USA. The five VWUs were representative of portable units that are for hire in the USA and differed in the combination of water volume (liters $minute^{-1}$ (l pm)) and pressure (kilograms of force $centimeter^{-1}$ (kgf/cm^2)) used in the washing process, and by their cost (Fleming, 2008). The combinations ranged from low volume – high pressure to high volume – low pressure (Fleming, 2008). All VWUs used mats underneath their washing area with a drain and pump that transported the material to the individual unit's filtering and containment system (Fig. 1 a, d). The VWU used in our seed accrual experiments was one of the systems evaluated.

To evaluate the efficacy of each VWU, the three types of vehicles were "dirtied" by being driven through a ~1.4 km test loop (638 m off-road and 742 m on unpaved/paved surfaces). The off-road section contained an artificially created mud bog (Fig. 1 b, c) that was re-wetted between vehicle runs. The unpaved section was scarified daily to maintain the loop in a similar condition for each vehicle type. Wheeled vehicles were driven around the test loop and underwent a 5 min VWU contractor wash. After the contractor wash, we (study personnel) completed a follow up wash to evaluate and record what the contractor VWU had missed. This sequence was repeated 18 times for each wheeled vehicle type, after which we performed a final, meticulous post-wash that included removing and cleaning the wheels. The soil waste from the 18 iterations for each vehicle type was aggregated, dried, weighed, and recorded by VWU contractor. We modified the contamination routine and methodology for the tracked vehicle, to represent their typical field use and wash routine. The tracked vehicles were driven once for each different VWU, only on the off-road section that included the mud bog, and had a long wash (60 min). Again, we completed a follow up wash to evaluate and record what the VWU contractor missed. The post-wash data, for each of the three vehicle types, represented the total amount of soil waste not removed by each of the five VWUs.

Each VWU had a different internal filtration and containment system process, therefore, seed survival could have been differentially affected depending on seed attributes. Thus, we evaluated the effect of the different vehicle wash units' filtration and collection methods on seed survival within the soil waste. We placed a known number of seeds from nine plant species in a known amount of soil and water, which was then subjected to the filtering and containment procedure of each VWU. The resulting soil and seed waste was transported back to the MSU Plant Growth Center, where our seed protocol was applied and emerging seedlings were monitored for 9 months. The nine species were *Agropyron trachycaulum, Avena sativa, Echinacea purpurea, Fagopyrum sagittatum*, *Kochia scoparia, Linum usitatissimum, Melilotus officinalis, Poa pratensis*, and *Sinapis alba*. *Avena sativa* (11 mm long caryopsis) has the largest and *K. scoparia* (1–2 mm long) the smallest seeds. Total seed abundance and rate of seed accrual values used for the ATV and vehicle studies were calculated using the seed survival results from the appropriate VWU.

2.2.1. Wash duration

We evaluated the effect of wash duration on vehicle decontamination, using our primary VWU. We applied a known amount of soil onto a 4WD truck and washed it five times consecutively. The duration of each wash was 3 min, giving a total wash duration of 15 min. The soil removed by each successive wash was collected, dried, and weighed. This process was replicated ten times (6 at MSU and 4 at Orchard Training Area). Using the same process, we also evaluated if the pattern of seed removal was the same as soil. This was accomplished by adding known amounts of seed *(A. sativa, F. sagittatum, L. usitatissimum, M. officinalis, P. pratensis,* and *S. alba)* and soil to a 4WD truck and evaluating the amount removed after

Fig. 1. The primary vehicle wash unit's (VWU) containment mats including raised edges, wheel racks, undercarriage washes and hand held wands are shown in a and d, and the artificially created mud bog used to evaluate VWU effectiveness is shown b and c. Vehicle types are as follows: 4WD (Humvee in a and truck in c), large 4WD in b, tracked - M1A1 tank in d.

each successive wash. This portion of the experiment was replicated four times at the Orchard Training Area site.

2.3. Statistical analysis

Our metrics of interest for both the ATV and different vehicle type seed accrual studies were seed accrual rate (1 or 100 km^{-1}), total abundance and species richness. For seed accrual rate and seed abundance (both log transformed) linear (ATV study) or general linear mixed effects models (vehicle type study) were employed. Species richness was analyzed using generalized linear models with a Poisson error distribution. We assessed the normality and heteroskedasticity of our data and transformed as necessary prior to performing the analyses.

For the ATV study, our fixed effects were surface (on- and off-trail), season (summer or fall), and nativity (native or non-native). The fixed effects for the vehicle study were vehicle type (ATV, 4WD, large 4WD, tracked) and nativity (native or non-native), with exercise and replicates nested within site as random effects. For the vehicle study, all but one exercise were performed under dry conditions so we restricted our main analyses to these data, unless otherwise stated. Tukey comparison of means was utilized to analyze differences between the different vehicle types. We also evaluated mean seeds accrued 100 km^{-1} for 4WD and tracked vehicles under wet and dry conditions (exercise 4 and 5) at Limestone Hills Training Area, but there was insufficient data for statistical analysis.

Finally, we performed additional analysis to evaluate richness by life history (annual, biennial, perennial), life form (grass, forb, shrub/tree) and seed characteristics (length was the only characteristic consistently available, though not for all species) among the different vehicle types and seed bank samples, from the Limestone Hills Training Area. Generalized linear models with poisson distribution, or quasipoisson distribution due to overdispersion, were used.

The mitigation experiments, including the amount of soil removed by the VWU contractors and the effect of the VWU filtration and containment process on seed survival, were both examined with analysis of variance. The proportion of soil and seed removed by successive washes was analyzed using general linear mixed effects models: using logit transformation to address normality and heteroscedasticity issues. The fixed effect in the model was vehicle type, while the random effect of wash number was nested within replicate and site. Tukey comparison of means was once again used to compare between the individual washes.

All analyses were completed using the statistical analysis program 'R', version 3.3.1.

3. Results

3.1. Seed accrual experiments

3.1.1. All-terrain vehicle study

All terrain vehicles driven off-trail accrued seeds at a higher rate per km driven (km^{-1}) than on-trail ($F_{(1,20)} = 113.20$; $p = 1.10$ E-09), with a higher rate of accumulation on drives during the fall than the summer ($F_{(1,20)} = 39.24$; $p = 4.08$ E-06), and more non-native seeds than native seeds ($F_{(1,20)} = 61.20$; $p = 1.64$ E-07; Fig. 2). The same pattern was observed for total seed abundance: more seeds were accrued off-trail than on-trail ($F_{(1,20)} = 113.05$; $p = 1.12$ E-09), and more non-native than native seeds were accrued ($F_{(1,20)} = 62.43$; $p = 1.47$ E-07).

Mean species richness accrual on the ATVs did not differ between summer (21) and fall (25), although more non-native (12.6) than native species (7.9) accrued on the ATVs ($X^2_{(1,20)} = 12.86$; $p = 0.0003$). Overall 87 species were observed from the ATV washes, most species were rare.

3.2. Seed accrual on wheeled and tracked vehicle types

The small 4WD vehicles were driven on two different road surfaces, the mean number of seeds accrued was higher on unpaved (361 seeds 100 km^{-1}) than paved (68 seeds 100 km^{-1}) dry surfaces ($F_{(1,5)} = 22.97$; $p = 0.004$). All vehicle types were driven primarily on dry unpaved roads and there were differences between vehicle types ($F_{(3,11)} = 4.84$, $p = 0.021$): 4WD accrued seeds at a rate of 420 seeds 100 km^{-1}, significantly more than on large 4WD (151 seeds 100 km^{-1}) and less than on the tracked vehicles (887 seeds 100 km^{-1}), ATVs did not differ from other vehicles. Further, results of Tukey post hoc comparison of means demonstrated that tracked vehicles accrued seeds at a higher rate than large 4WD ($p < 0.001$) but did not differ from the ATV (Fig. 3). The rate of seed accrual nor the abundance differed with nativity.

During our sampling of the military exercises there was a period of high precipitation. This provided us with the opportunity to compare seed accrual on 4WD and tracked vehicle types under wet versus dry conditions; we compared one wet and one dry exercise performed a week apart, in which multiple vehicles of each type were used. Unsurprisingly, more seeds were accrued under wet conditions for both tracked and the wheeled vehicles: the rate of accrual 100 km^{-1} increased under wet conditions 11.2 and 19.6-fold for tracked and wheeled vehicles, respectively.

Total species richness accrued on the different vehicle types was high for the two vehicle study sites (61 and 77 total species; Supplemental Table 1). Overall, total richness, native and non-

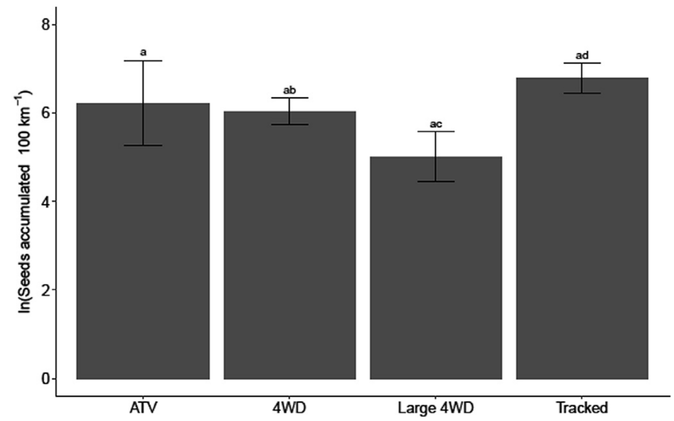

Fig. 3. Rate of seed accrual on four different vehicle types driven on unpaved roads. The bars represent standard errors, letters indicated differences ($p < 0.05$).

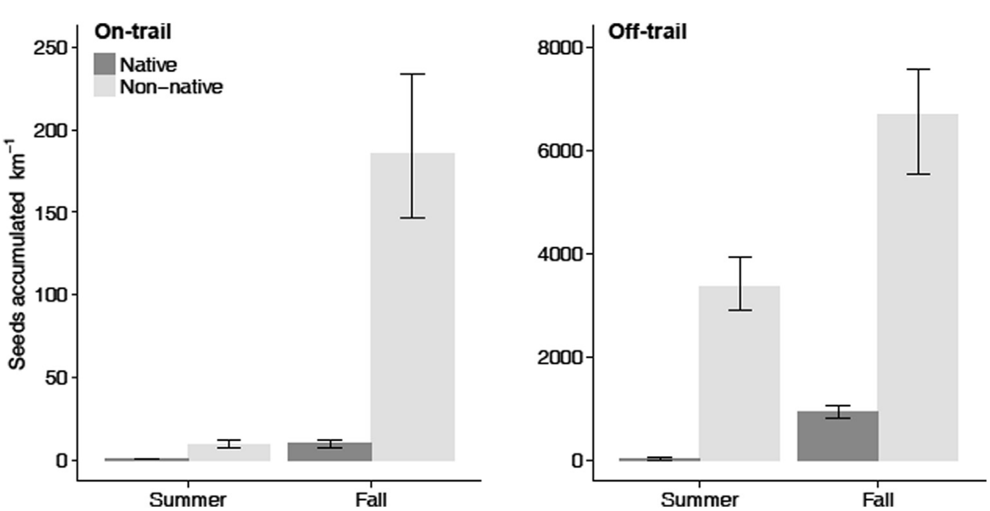

Fig. 2. Mean number of native and non-native seeds accumulated per kilometer for all terrain vehicles driven on- and off-trail in both summer and fall. Bars represent standard errors from three replicates of 24 vehicle laps (76.8 km). Note the different scales of the y-axis for the on- and off-trail data.

native richness did not differ among vehicle types nor the seed bank, at either site. Furthermore, the species accrued demonstrated different life history attributes (annual, biennial, perennial), forms (grass, forb, shrub) and seed lengths; and we evaluated differences with seed bank samples from the Limestone Hills Training Area. Annual and biennial richness did not differ among vehicle types and the seed bank, however, perennial richness did differ ($X^2_{(4,10)} = 16.82$; $p = 0.002$) with all vehicle types having lower richness than the seed bank. Forb and shrub richness did not differ either, but grass richness did ($X^2_{(4,10)} = 9.51$; $p = 0.049$) and was lower for 4WD ($p = 0.02$) and large 4WD ($p = 0.001$) than the seed bank. It should be noted that three-quarters of the grasses observed were perennial. Finally, we observed no difference in the length of the seeds accrued by the different vehicle types and the seed bank.

3.3. Vehicle wash unit studies

The mean soil waste removed by the VWU was 79% (±9.9%), with no differences among the vehicle types or wash units (Fig. 4). The percentage of seeds surviving the VWU containment and filtering procedure did not differ among the five VWU either, nor was there any difference among species. Overall seed survival was low (23% ± 9%).

3.3.1. Wash duration

The results of the five successive three-minute washes of a 4WD using our primary VWU demonstrated that 59% of the total soil waste was removed during the first three-minute wash, a further 19% during the second wash, and much less during the following three washes (11%, 7%, and 4% respectively; Fig. 5). The number of successive washes made the vehicle cleaner ($F_{(4,25)} = 90.61$; $p = 1.14$ E-14). Results of Tukey post hoc comparison of means demonstrated that the first three washes made the vehicle significantly cleaner ($p < 0.001$), however there was no difference in the mean cumulative percentage removed between the third and fourth consecutive washes ($p = 0.11$; Fig. 5).

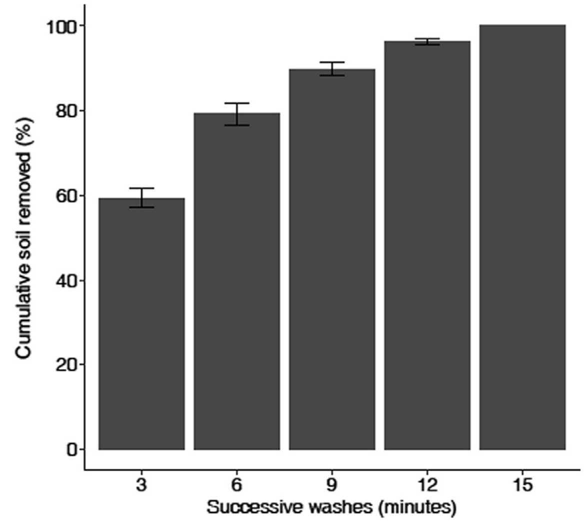

Fig. 5. Cumulative percentage of soil waste removed from a 4-wheel drive vehicle with five successive 3 min duration washes, using the primary vehicle wash unit.

4. Discussion

This is the first study to quantify the rate and magnitude of seed accrual by vehicles, adding critical data to the emerging research on the role of vehicles as dispersal vectors. Vehicles accrued seeds at higher rates than we expected, especially under dry conditions before the peak of seed shed, a period we expected to be relatively low risk. We demonstrate that vehicle accrual of plant propagules is

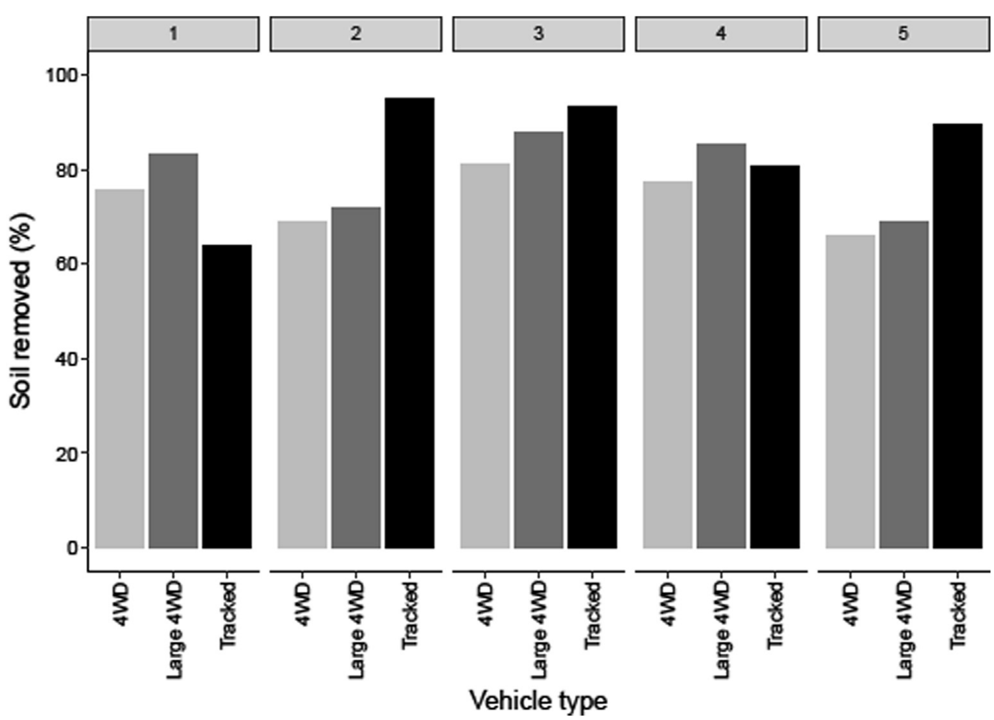

Fig. 4. The percentage of soil removed by the different vehicle wash units (1–5) for each vehicle type, assessed through our additional cleaning procedures. The data for the wheeled vehicle types (4WD, large 4WD) for each wash unit represents the combined wash total after driving a 1.4 km variable surface course 18 times; results of the tracked vehicle are from one drive over the unpaved section of the course.

affected by different driving surfaces (paved versus unpaved, and on-trail vs. off-trail), under different road conditions (wet and dry), and seasons (summer versus fall). The plant propagules accrued by vehicles are representative of a site's vegetation. This pattern of indiscriminate accrual demonstrates vehicles pose both a risk for dispersing non-native and invasive species but also play a role in moving native species into new areas. Spread of native species by vehicles may be beneficial to help address range shifts resulting from global climate change; especially with recent research demonstrating that not all ranges are poleward or upwards in elevation (Lenoir and Svenning, 2015). In addition, our evaluation of portable vehicle washing techniques demonstrates that we have existing technological solutions that can mitigate the threat of vehicle dispersal of problematic invasive plant species.

The ATV study highlights the importance of both driving surface and season for seed accumulation rates, with significantly greater accrual off-trail and in the fall compared with on-trail and in the summer. Previous studies have found that off-trail travel of various types (e.g. walking, horse-riding, camping, mountain biking, and vehicles) cause changes to the amount of litter, bare-ground, and soil conditions (e.g. erosion and altered nutrient levels) (Pickering and Hill, 2007). This has often resulted in changes to plant community composition (see reviews by: (Liddle, 1991; Pickering and Hill, 2007). By quantifying significant seed accrual by off-trail vehicles, our study has identified one mechanism through which off-trail driving results in altered plant community composition: vehicles driving off-trail/road scarify the soil, providing microsites favorable for plant establishment, while concurrently providing an abundance of seed, potentially non-native in origin. Pickering and Hill (2007) in their review demonstrated an increase in non-native invasive plant species associated with off-road travel in Australia.

Plants differ in their phenology and previous studies evaluating seed abundance from mud samples taken from vehicles (Clifford, 1959; Schmidt, 1989; Zwaenepoel et al., 2006) and seed accrual on different vectors (see Pickering and Hill (2007) for review) have found differences in the seasonality of seed accrual. Consistent with these studies and our expectations, we found seed accrual to be significantly higher in the fall than in the summer. This finding was exaggerated when seed accrual of the on- or off-road trials were compared; the most significant seed accrual occurred off-road during the fall. These findings would support travel restriction regulations that correspond to times (seasons) of seed set for species of concern (e.g. species considered especially invasive in the region), particularly for off-trail travel.

The importance of driving surface was also demonstrated in the vehicle type study, with higher seed accrual rates on unpaved than paved roads for 4WD (36 vs 7 km^{-1}, respectively) the only type driven on both surfaces. Furthermore, our study shows vehicle type matters. When comparing the rate of seed accrual of vehicles driven primarily on unpaved roads, seed accrual was higher for 4WD than large 4WD, and tracked vehicles accrued more than twice that of either 4WD or large 4WD. Overall, the rates of seed accrual were surprisingly high given the exercises were performed before yearly seed production began at our sites, when we would expect seed accrual to be at its lowest. As such, they represent a conservative estimate of seed accrual. Previous studies have estimated between 0.9 and 3 seeds per vehicle (Hodkinson and Thompson, 1997; Lonsdale and Lane, 1994; Zwaenepoel et al., 2006) but these studies did not wash entire vehicles; they sampled from the exterior of the vehicle and sometimes within it, and the distance driven prior to sampling was unknown. Our results indicate that vehicles driven primarily on unpaved roads pose a higher risk of gaining and dispersing non-native seeds than those driven on paved roads. Thus, all vehicles, tracked particularly, driven frequently on unpaved roads and more so off-road should be cleaned frequently, and especially before being driven into a new region or area of conservation value.

Unsurprisingly, we found that seed accrual was greater under wet conditions. Climate zone and seasonality are environmental factors that can affect the amount of damage done to vegetation by recreation (see Pickering and Hill, 2007). Our results empirically demonstrate that another consequence of driving in wet conditions is the accrual and subsequent dispersal of seeds. Again, this highlights the importance of restricting and regulating travel during sensitive time-periods and conditions. Taylor et al. (2012) observed more rapid seed loss from vehicles under wet conditions on paved than unpaved roads, and Zwaenepoel et al. (2006) observed less mud on vehicles as precipitation increased. Our results suggest that vehicles driven in muddy conditions will rapidly accrue seeds and, combined with Taylor et al.'s (2012) study, when these vehicles are then driven on paved roads they will disperse seeds over shorter distances than those vehicles driven on unpaved roads. Such information could be used to inform roadside vegetation monitoring programs after road construction and road improvement projects.

Species richness did not differ between vehicle types nor seed bank samples, suggesting it was representative of the surrounding vegetation. This was also true at our ATV sites, where we observed higher non-native than native species richness in both our vegetation survey and ATV samples (data not presented). Previous studies have observed similar richness between vehicle samples and the roadside and regional flora (Clifford, 1959; Schmidt, 1989; Zwaenepoel et al., 2006).

Our study and Schmidt's (1989) conclude that all types and sizes of seed are accrued on vehicles. We observed similar number of species with annual and biennial life histories, and forb and shrub functional forms, among vehicle types and the seed bank samples. We did observe less perennials from our vehicle samples, and less grass species (N.B. three-quarters of our grass species were perennial) on the two 4WD vehicle types, but we have no explanation for this pattern. Seed length did not differ among vehicle type samples nor the seed bank. Similarly, seed length didn't differ between vehicle samples and local roadside flora in previous studies (Clifford, 1959; Zwaenepoel et al., 2006), though it did differ from the regional flora (Zwaenepoel et al., 2006).

4.1. Using information on seed accrual to develop interception programs

In the USA, vehicle recreation (ATVs and others) on unpaved forest roads and off-road driving is increasing (Switalski et al., 2004), thus, developing land management policies to address dispersal of plant propagules via vehicles is important. Vehicle seed accrual can inform land management policies in two different ways. First, as suggested by Auffret and Cousins (2013), in areas where the roadside vegetation is native, vehicles can be valued for their ability to transport native seeds between fragmented habitats and mitigate global climate change. As the seed richness accrued by the vehicles in our study generally matched the surrounding flora, our results demonstrate the viability of such an endeavor provided appropriate steps are taken to ensure non-native species are not introduced and spread.

Second, if a goal of public land management, especially in conservation areas, is to limit the introduction of non-native plant species, an approach that takes into consideration the ability of vehicles to transport seeds should be considered. An approach such as this could be modelled on current programs that address the problem of invasive aquatic species being spread anthropogenically (Elwell and Phillips, 2016). The invasion of aquatic nuisance species, such as Dreissenid (quagga and zebra) mussels, into western USA has resulted in a watercraft interception program (Elwell and Phillips, 2016). This program has protocols and standards, which include random check points, screening interviews and assessments based on the history of the watercrafts, followed by inspections by trained professionals (Elwell and Phillips, 2016; Zook and Phillips, 2009). While the program isn't perfect and improvements are being made (Zook and Phillips, 2009), it demonstrates that approaches can be taken to mitigate invasion.

The portable vehicle wash units (VWUs) we tested removed ~80% of soil and other matter from dirty vehicles. While ~20% of seeds remain for dispersal, this is still a considerable reduction in the risk of seed dispersal and new invasions. We would recommend that fair to moderately muddy 4WD and large 4WD be washed for 6–9 min. Vehicle inspections, including screening interviews and assessments, and subsequent washing by VWUs in high risk areas (i.e. those with a high amount of known off-road/unpaved road travel or those with a high level of soil disturbance) and key conservation areas (e.g. National Parks and Monuments) would be a way to decrease seed spread. Given the effects of environmental factors on seed accrual, the VWU use should be linked with season and surface conditions. Another factor affecting the risk of vehicles introducing non-native plants is the distance that they have travelled and the type of road: wide, paved national roads with high traffic intensity have more non-native species than narrower, unpaved local roads with lower traffic intensity and local traffic (Vakhlamova et al., 2016). Thus, vehicles travelling longer distances between regions are more likely to introduce species that are non-native to the new area. Therefore, washing stations should be prioritized near conservation areas that people travel widely to visit and, during the screening process, vehicles that have driven greater distances should be prioritized for washing.

Consistent strategies to remove waste water and material is an issue for the watercraft interception programs (Zook and Phillips, 2009). Our findings demonstrate that the vehicle wash unit process of soil and seed containment, filtering, and removal, damages seeds. Evaluation of seed survival from the five vehicle wash units demonstrated that this process destroys ~77 percent of seeds. While containment and disposal strategies for soil and seed waste were not part of this study, it is apparent that storing the soil and seed waste prior to removal could destroy most of the seeds; one of the vehicle wash unit contractors placed their soil and seed waste in double wrapped black plastic before disposing at a landfill and ad hoc sampling from bags left on site for 3–4 weeks generated no seedlings in the greenhouse (Rew, unpublished). Thus, while further experimentation is needed, our findings suggest that if an invasive plant seed interception program is to be employed, the chance of soil and seed waste causing further risk of invasion can be minimized by storage in anaerobic conditions, on site or at public washing/inspection stations, prior to disposal.

5. Conclusions

Plant propagules accrue indiscriminately on all vehicles types. These results support the long-held paradigm of vehicles as seed dispersal vectors. Therefore, as universal plant dispersal vectors, vehicles provide a potential risk for new invasions or, conversely, a conservation technique for native species in exceptional situations. Seed accrual is affected by environmental factors (driving surface, surface conditions, and season), thus mitigating seed accrual and subsequent dispersal should vary temporally and spatially according to conditions. Finally, portable vehicle wash units are effective in the removal of soil and seed waste from dirty vehicles, provided the wash is of sufficient length ($\geq$6–9 min), very muddy vehicles will need longer washes. Similar to the watercraft interception programs, we recommend that non-native plant interception programs be employed during high risk times, in high risk areas, on high risk vehicles: consequently, vehicle wash units should be employed during wet times of year or after storms, especially when plants are shedding seeds, and near activities with high levels of soil disturbance (e.g. during wildfire control operations, utility installation) and surrounding areas of conservation interest (e.g. National Parks), and washing should focus on vehicles that have recently driven great distances, on unpaved surfaces, or off-road.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jenvman.2017.10.060.

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