ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/297441908

Waterfowl endozoochory: an overlooked long-distance dispersal vector for Cuscuta (dodder)

Article *in* American Journal of Botany · April 2016

Impact Factor: 2.6 · DOI: 10.3732/ajb.1500507

READS

20

6 authors, including:

Miguel A García

University of Toronto

48 PUBLICATIONS **1,165** CITATIONS

SEE PROFILE

Susan E.W. De La Cruz

United States Geological Survey

22 PUBLICATIONS **294** CITATIONS

SEE PROFILE

Andy J Green

Estación Biológica de Doñana

285 PUBLICATIONS **7,133** CITATIONS

SEE PROFILE

All in-text references underlined in blue are linked to publications on ResearchGate, letting you access and read them immediately.

Available from: Miguel A García
Retrieved on: 17 June 2016

RESEARCH ARTICLE

AMERICAN JOURNAL OF BOTANY

BRIEF COMMUNICATION

Waterfowl endozoochory: An overlooked long-distance dispersal mode for *Cuscuta* (dodder)[1]

Mihai Costea[2,7], Saša Stefanović[3], Miguel A. García[3], Susan De La Cruz[4], Michael L. Casazza[5], and Andy J. Green[6]

PREMISE OF THE STUDY: Dispersal of parasitic *Cuscuta* species (dodders) worldwide has been assumed to be largely anthropomorphic because their seeds do not match any previously known dispersal syndrome and no natural dispersal vectors have been reliably documented. However, the genus has a subcosmopolitan distribution and recent phylogeographic results have indicated that at least18 historical cases of long-distance dispersal (LDD) have occurred during its evolution. The objective of this study is to report the first LDD biological vector for *Cuscuta* seeds.

METHODS: Twelve northern pintails (*Anas acuta*) were collected from Suisun Marsh, California and the contents of their lowest part of the large intestine (rectum) were extracted and analyzed. Seed identification was done both morphologically and using a molecular approach. Extracted seeds were tested for germination and compared to seeds not subjected to gut passage to determine the extent of structural changes caused to the seed coat by passing through the digestive tract.

KEY RESULTS: Four hundred and twenty dodder seeds were found in the rectum of four northern pintails. From these, 411 seeds were identified as *Cuscuta campestris* and nine as most likely *C. pacifica*. The germination rate of *C. campestris* seeds after gut passage was 55%. Structural changes caused by the gut passage in both species were similar to those caused by an acid scarification.

CONCLUSIONS: Endozoochory by waterbirds may explain the historical LDD cases in the evolution of *Cuscuta*. This also suggests that current border quarantine measures may be insufficient to stopping spreading of dodder pests along migratory flyways.

KEY WORDS *Anas acuta*; Convolvulaceae; identification; invasive plants; long-distance dispersal; northern pintail; parasitic plants; pest; seed viability

"The dispersal of the Dodders to remote islands is very puzzling."
Ridley, 1930

Seeds of the parasitic plant genus *Cuscuta* (dodder) have been considered "unspecialized" or "non-adapted" because they lack a morphological dispersal syndrome (Ridley, 1930; Kuijt, 1969; Dawson et al., 1994; Costea and Tardif, 2006). Natural dispersal by wind (Lyshede, 1984) and water have been anecdotally suggested for a select number of species (reviewed by Dawson et al., 1994; Costea and Tardif, 2006), but there is no evidence to suggest that these vectors allow long-distance dispersal (LDD). No other natural dispersal vectors have been recognized for *Cuscuta* diaspores, although seeds have been repeatedly recorded in the diet of waterfowl (see Discussion). Yet the genus has a subcosmopolitan distribution and its nearly 200 species inhabit a great variety of habitats ranging from cold-temperate to tropical, riparian to desert, coastal to high mountains, grasslands, sand-dunes, forests, saline, vernal pools, ruderal, and agricultural (Yuncker, 1932; Costea et al., 2015b). Recent phylogeographic results have indicated that a minimum of 18 remarkable LDD events have occurred in the diversification of *Cuscuta* at different taxonomic levels, i.e., subgeneric, specific, and varietal (Stefanović et al., 2007; García et al., 2014). These LDD events inferred phylogenetically occurred a long time before the evolution of *Homo sapiens*, and until now all of them have been biologically inexplicable in view of the limited natural dispersal ability recognized for *Cuscuta* seeds. For example, the evolution of subg. *Grammica*, the largest infrageneric group of *Cuscuta* (ca. 150 sp.) distributed mostly in the Americas, most likely involved a transoceanic dispersal from South Africa to South America (Stefanović et al., 2007; García et al., 2014). LDD occurred subsequently from the

[1] Manuscript received 1 December 2015; revision accepted 1 March 2016.
[2] Department of Biology, Wilfrid Laurier University, Waterloo, Ontario N2L 3C5, Canada;
[3] Department of Biology, University of Toronto Mississauga, Mississauga, Ontario L5L 1C6, Canada;
[4] U.S. Geological Survey, Western Ecological Research Center, San Francisco Bay Estuary Field Station, 505 Azuar Drive, Vallejo, California 94592 .SA;
[5] U.S. Geological Survey, Western Ecological Research Center, Dixon Field Station, 800 Business Park Drive, Dixon, California 95620 .SA; and
[6] Wetland Ecology Department, Estación Biológica de Doñana (EBD-CSIC), Sevilla 41092 Spain
[7] Author for correspondence (e-mail: mcostea@wlu.ca)
doi:10.3732/ajb.1500507

North or South American *Grammica* clades to some islands and virtually to all the other continents; e.g., *C. gymnocarpa* Engelm. and *C. acuta* Engelm. to the Galapagos Islands (Costea et al., 2015a); *C. sandwichiana* Choisy to Hawaii; *C. tasmanica* Engelm. and *C. victoriana* Yunck. to Australia (Costea et al., 2013); *C. kilimanjari* Oliv. to eastern Africa; *C. hyalina* Roth. to Africa and Asia (Costea and Stefanović, 2010); *C. chinensis* Lam. (var. *chinensis*; Costea et al., 2011) and *C. australis* R.Br. to Asia (see more cases in García et al., 2014).

Numerous *Cuscuta* species are major global pests, capable of drastically reducing the yield of numerous agricultural/horticultural crops or invading natural ecosystems (Dawson et al., 1994; Parker and Riches, 1993). The long-distance movement of such dodder species has long been thought to take place exclusively via contaminated seeds of various crops or Asian herbal products (Beal, 1910; Knepper et al., 1990; Dawson et al., 1994; Costea and Tardif, 2006). As a result, most countries have adopted legislation measures for surveillance and quarantine at the border to prevent the introduction of foreign *Cuscuta* spp. within their territory (Costea and Tardif, 2006). It is therefore important to know if *Cuscuta* seeds can also undergo LDD via nonhuman vectors.

The objective of this short-note is to report for the first time the endozoochory of *Cuscuta* (dodder, Convolvulaceae) seeds by a migratory waterfowl (northern pintails *Anas acuta* L.; Anatidae), and to discuss the implications of this finding.

MATERIALS AND METHODS

As part of a broader study of seed dispersal by waterfowl in the San Francisco Bay area, 11 northern pintails (hereafter referred to as "pintails"), were collected from Wings Landing, Suisun Marsh, Solano Co., California, USA (38°13′31.63″N, 122°2′7.61″W). Pintails migrate from breeding grounds in Canada, Alaska, and Russia to winter in this area (Miller et al., 2005). Four birds were collected on 25 January 2015 and seven on 2 February 2015. After collection, birds were kept in a cooler on wet ice and dissected within 12 h. Collection of pintails was carried out under the guidance of the U.S. Geological Survey, Western Ecological Research Center's Animal Care and Use Committee (WERC-2015-01) with permits from California Department of Fish and Game (SCP #003855) and the U.S. Fish and Wildlife Service (MB #102896).

None of the pintails showed any signs of disease upon dissection. The lower alimentary canal from the small intestine to the cloaca was removed after sealing the external part of the cloaca with duct tape, and then placed in the refrigerator. Within one to four days of collection, the internal contents of the lowest part of the large intestine ("rectum" from hereon, 6–8 cm in length) were extracted by cutting off the intestine immediately below the caeca, then squeezing the contents into dechlorinated tap water. Being at the end of the digestive system, the rectum was selected for study to ensure that present seeds had completely survived the digestive process (Brochet et al., 2010a). The sample was washed through an 85 μm sieve then placed in a petri dish for inspection under the binocular microscope. Seeds were removed, classified, and counted. To test their viability, 80 morphologically similar seeds extracted from an individual pintail labeled NOPI 29 were placed for germination on 3 February 2015 and checked twice a week until 2 April 2015 when the germination trial was terminated. Seeds were placed at room temperature (minimum 21°C and maximum 25°C) in a sunlit window on filter paper placed on top of a layer of cardboard soaked in distilled water inside petri dishes.

Another 20 seeds, similar morphologically to the ones used above, were kept dry and germinated on 15 May at the University of Toronto, Mississauga. The seven seedlings produced (six from NOPI 29 and one from a different bird labeled NOPI 30) were used to identify the dodder species. Five of these seedlings were identified through DNA barcoding, using ITS (nuclear) and *trnL-F* (plastid) DNA sequences. Seedlings were frozen in liquid nitrogen and pulverized using solid glass beads (3 and 6 mm; Fisher Scientific, Waltham, Massachusetts, USA) and a mixer mill (MM 300, Retcsh GmbH (Haan, Germany); 1 min at 30 Hz). DNA extractions, polymerase chain reaction (PCR) reagents and conditions, and amplicon purifications followed the protocols detailed in Stefanović et al. (2007). Cleaned PCR products were sequenced at the McGill University and Génome Québec Innovation Centre (Montreal, Quebec, Canada). A total of four ITS and six *trnL-F* sequences were analyzed and deposited in GenBank (accession numbers KU761496–KU761506). Sequences were aligned manually using Se-Al version 2.0a11 (Rambaut, 2002) and compared with our database containing a large number of *Cuscuta* species from the subgenus *Grammica* used in our previous broad-scale phylogenetic analyses of this group (Stefanović et al., 2007; Stefanović and Costea, 2008), as well as more recent analyses targeting specifically the *Cuscuta pentagona* Engelm./*campestris* species group (Costea et al., 2015a). To further characterize newly obtained DNA sequences, we compared them with those deposited in Genbank using BLAST. The remaining sixth seedling from NOPI 29 was grown using *Plectranthus scutellarioides* (L.) R.Br. (Lamiaceae) as a host in the University of Toronto, Mississauga greenhouse. At maturity, flowers of this dodder specimen were collected, dissected, and examined to identify the species morphologically. Vouchers of this plant were deposited in the TRTE and WLU herbaria as NOPI 29-7, 2 August 2015, *García s.n.* (herbarium voucher at TRTE and spirit specimen at WLU).

Morphology of all the seeds was initially surveyed with a Nikon SMZ1500 stereomicroscope. Thirty of the 320 remaining *Cuscuta* seeds were rehydrated and examined to determine the extent of morphological and structural changes caused by their passing through the digestive tract of pintails. Subsequently, seeds were cut in half through the hilar region, perpendicular to the hilum scar, subjected to a hexamethyldisilazane (HMDS) treatment as an alternative method to critical point drying (Wright et al., 2011), mounted on specimen stubs, and coated with 30 nm of gold using an Emitech K550 sputter coater (Quorum Technologies, Lewes, UK). Examination of the surface and seed coat structure was conducted with a Hitachi SU-1500 Scanning Electron Microscope (SEM) at 3 KV. Seeds were compared to those in a morphological database of *Cuscuta* seeds (Costea, unpublished data) after a search of the dodder species present at Suisun Marsh (Vasey et al., 2012; Consortium of California Herbaria, 2016).

After the identification of the seeds retrieved from the pintails (see Results below), typical dodder seeds of the same species that had not been subjected to gut passage were prepared and examined as indicated above from the following herbarium specimens: (1) *Cuscuta campestris*: USA, California, Sonoma Co., September 2007, *Cadman et al. 2832* (WLU); (2) Riverside Co., 28 July 1994, *Sanders 15174* (UCR); (3) San Bernardino Co., 1 September 2000, *Provance 2227B* (UCR); (4) *Cuscuta pacifica* Costea and M.A.R. Wright: USA, California, Humboldt Co., 28 August 1941, *C.C. and S.K. Harris 1175*

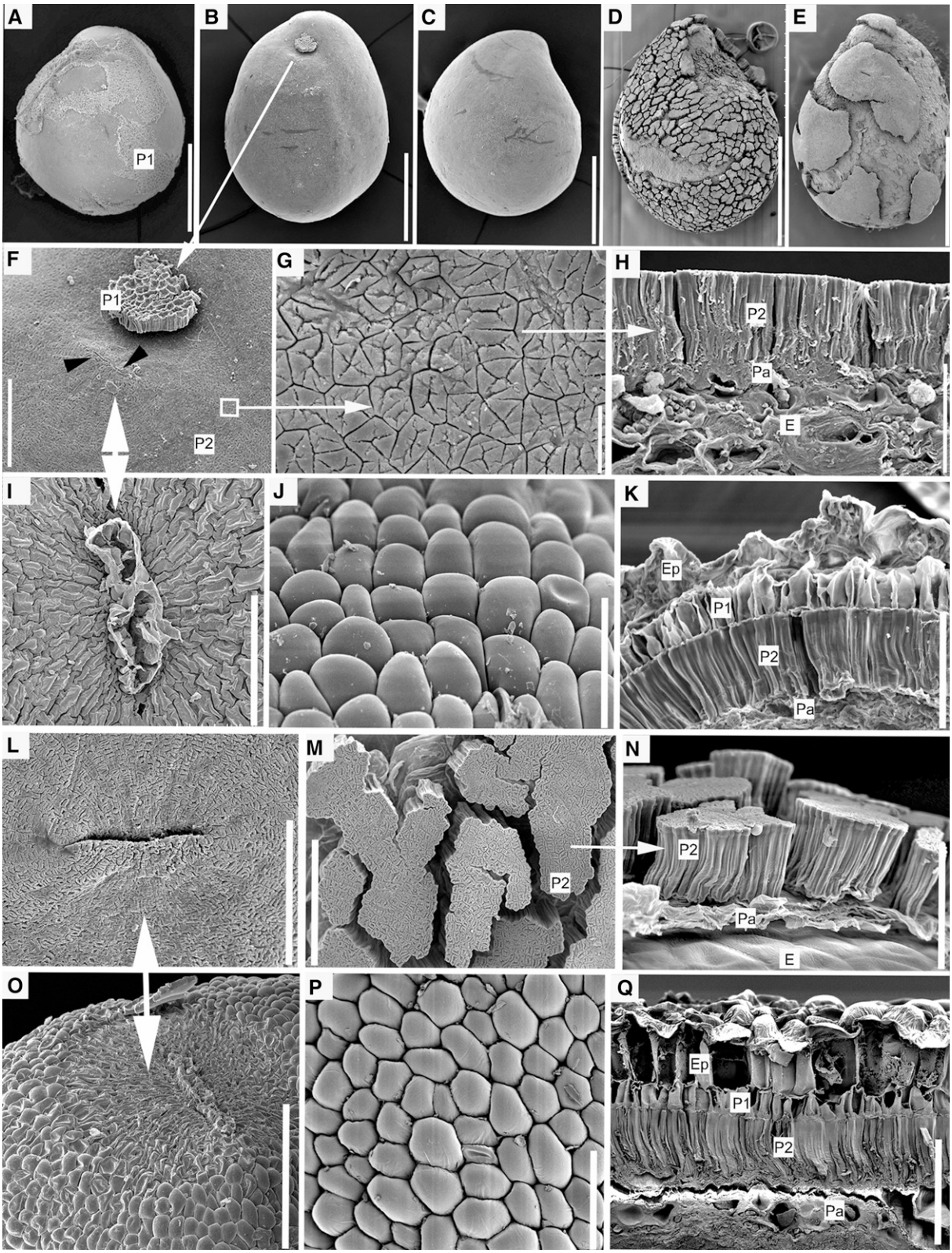

FIGURE 1 Morphological and structural changes caused by the passing of *Cuscuta* seeds through the digestive tract of northern pintail. (A-C) Passed seeds of *C. campestris*; note that the external palisade layer persisted on irregular portions of the seed (A), in the hilum area (B), or it was completely eliminated. (D, E) Passed seeds of *C. pacifica*; the seed coat is fragmented and the external palisade layer was entirely removed. (F-H) Surface detail and anatomy of seed coat in passed seeds of *C. campestris*: (F) Hilum area (black arrows delineate the hilum); (G, H) Sclereids of the internal palisade layer were brought to the surface of the seed coat because the epidermis and external palisade layer were entirely digested. (I-K) Surface detail and structure

(DAO); (5) Solano Co., 8 December 1959, *Crampton 5472* (CAS); and (6) Oregon, Lincoln Co., 30 July 1995, *Halse 4961* (NY).

RESULTS

Of the 11 pintails collected from Suisun Marsh, four of them had intact *Cuscuta* seeds in the rectum. Two individuals had a single seed, one individual (NOPI 30) had six seeds, and the fourth individual (NOPI 29) had 412 seeds. The majority of *Cuscuta* seeds were small, 0.7–1.2 mm long. However, nine of the *Cuscuta* seeds examined from NOPI 29 were larger, 1.4–1.9 mm long, indicating that two different dodder species had been ingested by this individual.

Barcoding showed that the small dodder seeds found inside the rectum of pintails belong to *Cuscuta campestris* (field dodder). All sequences generated in this study (four ITS and six *trnL-F*) were either identical to or had ≤ 2bp differences compared with those of *C. campestris* obtained for our previous studies (Stefanović et al., 2007; Stefanović and Costea, 2008; Costea et al., 2015a). Also, the BLAST search of online DNA databases showed that the sequences from the seedlings are compatible with *C. campestris*, with the highest scores having 100% query coverage and 99–100% identity with *C. campestris* and other closely related members of the *C. campestris/pentagona* species group. The same species identity, *C. campestris*, was obtained through the morphological examination of dissected flowers produced by the mature *Cuscuta* plant grown in the greenhouse. The nine larger seeds found in NOPI 29 were identified morphologically as most likely belonging to *C. pacifica* (Pacific salt-marsh dodder).

All the 80 seeds tested for viability belonged to *Cuscuta campestris*: 23 seeds germinated by 9 February (28.75%), and 44 by 23 March (55%). Germination of the nine seeds of *C. pacifica* was not tested because of their insufficient number. The passage through the digestive tract of pintails modified significantly the structure of the seed coat in both *Cuscuta* species (Fig. 1). In *C. campestris*, the seed coat maintained its integrity, remaining attached to the endosperm (Fig. 1A-C); in *C. pacifica* the seed coat fragmented and detached from the endosperm (Fig. 1D, E). In both species, the epidermis with dome-like cells, which is always present in seeds not subjected to gut passage (Fig. 1J, P), was entirely stripped out. The external palisade layer, also characteristic to *Cuscuta* seeds (Fig. 1K, R), was entirely digested in *C. pacifica* (Figs. 1D, E, M, N), and partially or totally eliminated in *C. campestris* (Figs. 1A-C, G, H). Remnants of the external palisade layer may persist on irregular surfaces in *C. campestris* (Fig. 1A), but most often it can be found only in concave areas or in the hilar zone (Fig. 1B, F). Thus, in both dodder species, after the digestion process, the testa was reduced to the internal palisade layer, which was brought to the surface of seeds (Fig. 1G, H, M, N). Also, in both species, the hilum, which is responsible for imbibition in *Cuscuta*, becomes completely exposed, i.e., visible as a nearly invisible line in *C. campestris* (Fig. 1F; compare with 1I), and more conspicuous in *C. pacifica* (Fig. 1L; compare with 1O).

DISCUSSION

Zoochory has not previously been proposed as a dispersal mode for *Cuscuta*, but in retrospect the existing literature provides much support for our finding since *Cuscuta* spp. seeds have already been reported in the diets of several species of migratory waterfowl (Cottam, 1939; Martin and Uhler, 1939; Chamberlain, 1959; Goodrick, 1979) and shore birds (Beltzer, 1991). However, none of these studies identified the *Cuscuta* species involved or tested the viability of passed seeds. In this study, the seeds of *C. campestris* retrieved after gut passage were viable and germinated at rates comparable to those reported for scarified seeds of this species at 21–24°C (e.g., Hutchison and Ashton, 1980; Benvenuti et al., 2005). Dormancy of *Cuscuta* seeds is physical, imposed by the impermeable seed coat with two palisade layers (e.g., Hutchison and Ashton, 1979; Lyshede, 1984; Jayasuriya et al., 2008). The structural changes reported after gut passage, especially the fragmentation of the seed coat in *C. pacifica*, are similar to those observed in *Cuscuta* after sulfuric acid scarification (Costea, unpublished data). Although we only found small numbers of seeds in three of the four ducks where *Cuscuta* was present, we only inspected a short section of the hindgut which holds a very small proportion of seeds carried through the entire digestive system (Brochet et al., 2010a).

Waterbirds provide a major ecosystem service by dispersing plants that lack a fleshy fruit and hence are not dispersed by frugivores (Green and Elmberg, 2014). The potential of migratory waterbirds to disperse plants over long distances and to oceanic islands has long been recognized (Darwin, 1859; Proctor, 1968; Carlquist, 1967). Experimental and field studies suggest that waterfowl are major but largely overlooked vectors for a broad range of wetland and terrestrial plants, including many species with "non-adapted" seeds like *Cuscuta* (Brochet et al., 2009, 2010b; Soons et al., 2016). Dodder seeds or fruits may be washed into wetlands by rainfall, making them available to dabbling ducks such as pintails. Modeling confirmed that dabbling ducks readily disperse seeds over hundreds of kilometers or more (Viana et al., 2013). Among other Convolvulaceae with subcosmopolitan distribution, Proctor (1968) showed experimentally that viable seeds of *Convolvulus arvensis* L. can be retained in the gut of shore birds for up to 144 h, which would be enough to cross the Pacific Ocean (Gill et al., 2009). Thus, as previously suggested for fleshy-fruited plants (e.g., Popp et al., 2011), our findings indicate that waterbirds or shore birds may explain the historical LDD events that took place in the evolution of *Cuscuta*.

Pintails wintering in California, Mexico, the Caribbean, and Central America undertake rapid long-distance migratory movements northwards to various parts of North America and Russia (Miller et al., 2005; Arzel et al., 2006). Similarly, pintails wintering in the Mediterranean Basin and Africa or in southeastern Asia (e.g., Japan) migrate to various northern areas of Europe and Asia (Arzel et al., 2006; Hupp et al., 2011). Although northern pintail migration routes are usually not transoceanic, vagrants occasionally

of seed coat in *C. campestris* seeds not subjected to gut passage: (I) Hilum is quite visible; (J) Epidermis with dome-like cells; (K) Anatomy of complete seed coat (with epidermis and external palisade layer). (L-N) Surface detail and structure of seed coat in passed *C. pacifica* seeds: Hilum (L) is more visible than in *C. campestris*; internal palisade layer fragments and seed coat detach from endosperm (M, N). (O-R) Surface detail and anatomy of seed coat of *C. pacifica* seeds not subjected to gut passage. Notes: P1 = external palisade layer; P2 = internal palisade layer; Pa = parenchyma; Ep = epidermis; E = endosperm. Scale bars: A-C, 0.5 mm; D, E, 1 mm; F, I, L, M, O, 100 µm; H, J, K, N, P, R, 50 µm; G, 10 µm.

cross the Atlantic or Pacific (e.g., Flint et al., 2009). However, this particular duck species is probably not the dispersal vector involved in most historical LDD events that took place in the evolution of *Cuscuta*. One possible exception is *C. sandwichiana*, which is part of a North American clade but is endemic to Hawaii (García et al., 2014; Costea et al., 2015b), where pintails winter regularly (e.g., Udvardy and Engilis, 2001). Endozoochory by shore birds is the most likely explanation for other historical LDD events (Carlquist, 1967).

Cuscuta pacifica is the typical dodder of saline tidal marshes on the Pacific Coast (Costea et al., 2009), including at Suisun Marsh (Barbour, 2007; Vasey et al., 2012, referred to as "*C. salina*"). *Cuscuta subinclusa* Durand & Hilg., a closely related species (Costea et al., 2009), which is also present in the area (Vasey et al., 2012; Consortium of California Herbaria, 2016), has similar seeds morphologically (Costea et al., 2006) but it grows mostly on shrubs and trees. The seeds of all three *Cuscuta* species are enclosed in indehiscent fruits, which are usually persistent on the hosts in dense infructescences until the spring. For these reasons, it is more likely that the large seeds belong to *C. pacifica* which, like *C. campestris*, parasitize herbaceous hosts (Costea et al., 2009) and their fruits are more accessible to pintails feeding at ground level. Although this is not one of the LDD cases highlighted by García et al. (2014), the dispersal of *C. pacifica* over 2000 km of coast from British Columbia, Canada, via Washington, Oregon, and California in the USA, to Baja California in Mexico, may have involved pintails or other migratory waterbirds.

Cuscuta campestris is perhaps the most common weedy dodder worldwide (Costea et al., 2015a), and its ubiquitous presence has until now been considered to be explained solely as a result of human dispersal through contaminated seed crops. Our findings suggest that avian endozoochory may have also contributed to the widespread distribution of this species. For example, in this study the presence at Suisun Marsh shows that *C. campestris* movement is not necessarily linked to agricultural practices. Ducks have probably dispersed field dodder (and perhaps other species) within North America, Europe, and Asia. It has been recently reported (Costea et al., 2015a) that *C. gymnocarpa*, which is endemic to the Galapagos, is in fact a form of *C. campestris* that has evolved in the archipelago after a LDD event from the mainland. Thus, the possibility of endozoochory opens a new direction of research in the ecology and biogeography of *Cuscuta*. Finally, the potential for endozoochory reported here suggests that enforcement of the current border quarantine measures will not be sufficient to completely curtail the international movement of field dodder and other *Cuscuta* pest species.

ACKNOWLEDGEMENTS

A.J. Green received financial support through the Severo Ochoa Program for Centers of Excellence in R+D+I (SEV-2012-0262). M. Costea and S. Stefanović gratefully acknowledge financial support from NSERC of Canada Discovery grants (327013 and 326439, respectively). Field work was supported by the USGS Western Ecological Research Center through the Ecosystems Mission Area program. Kyle Spragens, Mason Hill, Jessica Donald, Vivian Bui, and Cory Overton provided essential help collecting and processing samples. Ádám Lovas-Kiss provided vital assistance in the initial identification of the *Cuscuta* seeds. Cory Overton and two anonymous reviewers reviewed the manuscript and kindly provided comments that improved the quality of the article. The use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

Arzel, C., J. Elmberg, and M. Guillemain. 2006. Ecology of spring-migrating Anatidae: A review. *Journal für Ornithologie* 147: 167–184.

Barbour, M. G. [ed.]. 2007. Terrestrial vegetation of California, 3rd ed., University of California Press, Berkeley, California, USA.

Beal, W. J. 1910. Seeds of Michigan weeds. Bulletin 260, Division of Botany, Michigan State Agricultural College, East Lansing, Michigan, USA.

Beltzer, A. H. 1991. Aspects of the foraging ecology of the waders *Tringa flavipes, Calidris fuscicollis* and *Charadrius collaris* (Aves: Scolopacidae; Charadriidae) in Del Cristal Pond (Santa Fé, Argentine). *Studies on Neotropical Fauna and Environment* 26: 65–73.

Benvenuti, S., G. Dinelli, A. Bonetti, and P. Catizone. 2005. Germination ecology, emergence and host detection in *Cuscuta campestris. Weed Research* 45: 270–278.

Brochet, A. L., M. Guillemain, H. Fritz, M. Gauthier-Clerc, and A. J. Green. 2009. The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe. *Ecography* 32: 919–928.

Brochet, A. L., M. Guillemain, H. Fritz, M. Gauthier-Clerc, and A. J. Green. 2010a. Plant dispersal by teal (*Anas crecca*) in the Camargue: Duck guts are more important than their feet. *Freshwater Biology* 55: 1262–1273.

Brochet, A. L., M. Guillemain, M. Gauthier-Clerc, H. Fritz, and A. J. Green. 2010b. Endozoochory of Mediterranean aquatic plant seeds by teal after a period of desiccation: Determinants of seed survival and influence of retention time on germinability and viability. *Aquatic Botany* 93: 99–106.

Carlquist, S. 1967. Biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. *Bulletin of the Torrey Botanical Club* 94: 129–162.

Chamberlain, J. L. 1959. Gulf coast marsh vegetation as food of wintering waterfowl. *Journal of Wildlife Management* 23: 97–102.

Consortium of California Herbaria. 2016. Data provided by the participants of the Consortium of California Herbaria. Website: *ucjeps.berkeley.edu/consortium* [accessed 23 February 2016].

Costea, M., M. A. García, K. Baute, and S. Stefanović. 2015a. Entangled evolutionary history of *Cuscuta pentagona* clade: A story involving hybridization and Darwin in the Galapagos. *Taxon* 64: 1225–1242.

Costea, M., M. A. García, and S. Stefanović. 2015b. A phylogenetically based infrageneric classification of the parasitic plant genus *Cuscuta* (dodders, Convolvulaceae). *Systematic Botany* 40: 269–285.

Costea, M., I. García Ruiz, K. Docksteder, and S. Stefanović. 2013. More problems despite bigger flowers: Systematics of *Cuscuta tinctoria* clade (subgenus *Grammica*, Convolvulaceae) with description of six new species. *Systematic Botany* 38: 1160–1187.

Costea, M., G. L. Nesom, and S. Stefanović. 2006. Taxonomy of the *Cuscuta salina-californica* complex (Convolvulaceae). *SIDA; Contributions to Botany* 22: 177–195.

Costea, M., I. Spence, and S. Stefanović. 2011. Systematics of *Cuscuta chinensis* species complex (subgenus *Grammica*, Convolvulaceae): Evidence for long-distance dispersal and one new species. *Organisms, Diversity & Evolution* 11: 373–386.

Costea, M., and S. Stefanović. 2010. Evolutionary history and taxonomy of the *Cuscuta umbellata* complex (Convolvulaceae): Evidence of extensive hybridization from discordant nuclear and plastid phylogenies. *Taxon* 59: 1783–1800.

Costea, M., and F. J. Tardif. 2006. Biology of Canadian weeds. *Cuscuta campestris* Yuncker, *C. gronovii* Willd. ex Schult., *C. umbrosa* Beyr. ex Hook., *C. epithymum* (L.) L. and *C. epilinum* Weihe. *Canadian Journal of Plant Science* 86: 293–316.

Costea, M., M. A. Wright, and S. Stefanovic. 2009. Untangling the systematics of salt marsh dodders: *Cuscuta pacifica*, a new segregate species from *Cuscuta salina* (Convolvulaceae). *Systematic Botany* 34: 787–795.

Cottam, C. 1939. Food habits of North American ducks. Technical Bulletin 643, 1-129.U.S. Department of Agriculture, Washington, District of Columbia, USA.

Darwin, C. 1859. The origin of species by means of natural selection, 1st ed. John Murray, London, UK.

Dawson, J. H., L. J. Musselman, P. Wolswinkel, and I. Dörr. 1994. Biology and control of *Cuscuta*. *Reviews of Weed Science* 6: 265–317.

Flint, P. L., K. Ozaki, J. M. Pearce, B. Guzzetti, H. Higuchi, J. P. Fleskes, T. Shimada, and D. V. Derksen. 2009. Breeding-season sympatry facilitates genetic exchange among allopatric wintering populations of northern pintails in Japan and California. *Condor* 111: 591–598.

García, M. A., M. Costea, M. Kuzmina, and S. Stefanović. 2014. Phylogeny, character evolution, and biogeography of *Cuscuta* (dodders; Convolvulaceae) inferred from coding plastid and nuclear sequences. *American Journal of Botany* 101: 670–690.

Gill, R. E., L. T. Tibbitts, C. D. Douglas, M. C. Handel, M. D. Mulcahy, C. J. Gottschalck, N. Warnock, et al. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: Ecological corridor rather than barrier? *Proceedings of the Royal Society of London, B, Biological Sciences* 276: 447–457.

Goodrick, G. N. 1979. Food of the black duck and grey teal in coastal northern New South Wales. *Wildlife Research* 6: 319–324.

Green, A. J., and J. Elmberg. 2014. Ecosystem services provided by waterbirds. *Biological Reviews of the Cambridge Philosophical Society* 89: 105–122.

Hupp, J. W., N. Yamaguchi, P. L. Flint, J. M. Pearce, K. I. Tokita, T. Shimada, M. A. Ramey, et al. 2011. Variation in spring migration routes and breeding distribution of northern pintails *Anas acuta* that winter in Japan. *Journal of Avian Biology* 42: 289–300.

Hutchison, J. M., and F. M. Ashton. 1979. Effect of desiccation and scarification on the permeability and structure of the seed coat of *Cuscuta campestris*. *American Journal of Botany* 66: 40–46.

Hutchison, J. M., and F. M. Ashton. 1980. Germination of field dodder (*Cuscuta campestris*). *Weed Science* 28: 330–333.

Jayasuriya, K. G., J. M. Baskin, R. L. Geneve, C. C. Baskin, and C. T. Chien. 2008. Physical dormancy in seeds of the holoparasitic angiosperm *Cuscuta australis* (Convolvulaceae, Cuscuteae): Dormancy-breaking requirements, anatomy of the water gap and sensitivity cycling. *Annals of Botany* 102: 39–48.

Knepper, D. A., R. A. Creager, and L. J. Musselman. 1990. Identifying dodder seed as contaminants in seed shipments. *Seed Science and Technology* 18: 731–741.

Kuijt, J. 1969. The biology of parasitic flowering plants. University of California Press, Berkeley, California, USA.

Lyshede, O. B. 1984. Seed structure and germination in *Cuscuta pedicellata* with some notes on *C. campestris*. *Nordic Journal of Botany* 4: 669–674.

Martin, A. C., and F. M. Uhler. 1939. Food of game ducks in the United States and Canada. Technical Bulletin 634. U.S. Department of Agriculture, Washington, District of Columbia, USA.

Miller, M. R., J. Y. Takekawa, J. P. Fleskes, D. L. Orthmeyer, M. L. Casazza, and W. M. Perry. 2005. Spring migration of northern pintails from California's Central Valley wintering area tracked with satellite telemetry: Routes, timing, and destinations. *Canadian Journal of Zoology* 83: 1314–1332.

Parker, C., and C. Riches. 1993. Parasitic weeds of the world: Biology and control. CAB International, Wallingford, UK.

Popp, M., V. Mirre, and C. Brochmann. 2011. A single mid-pleistocene long-distance dispersal by a bird can explain the extreme bipolar disjunction in crowberries (*Empetrum*). *Proceedings of the National Academy of Sciences* 108: 6520–6525.

Proctor, V. W. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. *Science* 160: 321–322.

Rambaut, A. 2002. Se-Al sequence alignment editor, version 2.0a11. University of Oxford, Oxford, UK.

Ridley, H. N. 1930. Dispersal of plants throughout the world. L. Reeve & Co., Ashford, UK

Soons, M., A. L. Brochet, E. Kleyheeg, and A. J. Green. 2016. Seed dispersal by dabbling ducks: An overlooked dispersal pathway for a broad spectrum of plant species. *Journal of Ecology* 104: 443–455.

Stefanović, S., and M. Costea. 2008. Reticulate evolution in the parasitic genus *Cuscuta* (Convolvulaceae): Over and over again. *Botany* 86: 791–808.

Stefanović, S., M. Kuzmina, and M. Costea. 2007. Delimitation of major lineages within *Cuscuta* subgenus *Grammica* (dodders; Convolvulaceae) using plastid and nuclear DNA sequences. *American Journal of Botany* 94: 568–589.

Udvardy, M. D., and A. Engilis. 2001. Migration of Northern Pintail across the Pacific with reference to the Hawaiian Islands. *Studies in Avian Biology* 22: 124–132.

Vasey, M. C., V. T. Parker, J. C. Callaway, E. R. Herbert, and L. M. Schile. 2012. Tidal wetland vegetation in the San Francisco Bay-Delta estuary. *San Francisco Estuary and Watershed Science* 10(2): 1–16. Website http://escholarship.org/uc/item/44z5v7xf

Viana, D. S., L. Santamaria, T. C. Michot, and J. Figuerola. 2013. Migratory strategies of waterbirds shape the continental-scale dispersal of aquatic organisms. *Ecography* 36: 430–438.

Wright, M. A., M. Welsh, and M. Costea. 2011. Diversity and evolution of the gynoecium in *Cuscuta* (dodders, Convolvulaceae) in relation to their reproductive biology: two styles are better than one. *Plant Systematics and Evolution* 296: 51–76.

Yuncker, T. G. 1932. The genus *Cuscuta*. *Memoirs of the Torrey Botanical Club* 18: 113–331.