

Hare don't care! Consumption of a rare, desert milkweed containing phytochemicals by the black-tailed jackrabbit

Steven M. Grodsky^{a,b,*}, Leslie S. Saul-Gershenz^{b,c}, Kara A. Moore-O'Leary^{d,1}, Jason P. Whitney^a, Rebecca R. Hernandez^{a,b}

^a Department of Land, Air & Water Resources, University of California, Davis, Davis, CA, 95616, USA

^b Wild Energy Initiative, John Muir Institute of the Environment, Davis, CA, 95616, USA

^c Department of Entomology and Nematology, University of California, Davis, CA, 95616, USA

^d Center for Population Biology, University of California, Davis, Davis, CA, 95616, USA



ARTICLE INFO

Keywords:

Asclepias
Cardenolides
Danaus
Herbivory
Lepus californicus
Mojave desert
Phytochemicals

ABSTRACT

We recorded video providing the first conclusive evidence that the black-tailed jackrabbit (*Lepus californicus*) consumes Mojave milkweed (*Asclepias nyctaginifolia*) containing phytochemicals in the Ivanpah Valley, Mojave Desert, California, USA. We discuss possible chemical and biological interactions between the black-tailed jackrabbit and Mojave milkweed. We explore potential ecological effects of black-tailed jackrabbit herbivory on Mojave milkweed, including competition with the monarch butterfly (*Danaus plexippus*) and its close relative the queen butterfly (*Danaus gilippus*), and how these ecological interactions may be affected by anthropogenic land-use and land-cover change in arid environments of the western United States.

1. Short communication

Nutrient and moisture limitations in arid environments typically favor plants with slow growth rates and seasonal emergence, both of which often equate to large investments in antiherbivore defenses (Coley et al., 1985). Meanwhile, desert herbivores rely on plants for nourishment. Given the rarity of perennial and freestanding water in arid environments, desert herbivores meet their physiological water requirements largely by consuming plant material. Over evolutionary time, the desert environment has intertwined plants and herbivores in a food web of ecological and chemical interactions; grazing pressure by herbivores has led to development and adaptation of plant antiherbivore defenses, and herbivores have, in turn, made physiological, behavioral, and dietary adjustments to tolerate plant secondary compounds (Cates and Rhoades, 1977; Meyer and Karasov, 1991). Our understanding of the chemical relationships between herbivores and antiherbivore plant defense syndromes predominantly stems from research investigating plant-insect interactions (Agrawal and Fishbien, 2006). Further, most studies of the chemical aspects of herbivory in arid environments by desert herbivores, especially rodents, have been conducted in laboratory experiments (see Meyer and Karasov, 1991) but few of these studies have been corroborated by field observations.

In desert and semidesert regions of North America, the black-tailed jackrabbit (*Lepus californicus*) often is the most important herbivore by animal biomass (Chew and Chew, 1970) (Fig. 1A). The diet of the black-tailed jackrabbit varies seasonally. In spring and early summer, black-tailed jackrabbits primarily consume high-protein (i.e., relatively high nitrogen and phosphorous) grasses (*Bromus* spp., *Stipa* spp., *Hilaria* spp.) and forbs (*Chaenactis* spp., *Sphaeralcea* spp.) (Simes et al., 2015). However, black-tailed jackrabbits eat the woody stems and branches of evergreen perennials during periods of resource scarcity, including the winter and summer in the Mojave Desert and the fall and winter in the Utah Great Basin (Currie and Goodwin, 1966; Hayden, 1966; Nagy et al., 1976). Many woody perennial plants consumed by the black-tailed jackrabbit in arid environments contain large amounts of secondary metabolites, including terpenoids (*Artemisia* spp.), phenolic resins (*Larrea tridentata*), tannins (*Coleogyne ramosissima*), saponins (*Atriplex* spp.), and monoterpenes (*Ericameria* spp.) (summarized in Meyer and Karasov, 1991). In contrast, short-lived and fast-growing herbaceous plants in arid environments theoretically have fewer chemical defenses in comparison to slow-growing perennials (*sensu* Coley et al., 1985), although some grasses possess secondary metabolites, toxin producing endophytic fungi, and silicon as defenses against mammalian herbivores (Huitu et al., 2014). The black-tailed jackrabbit possesses

* Corresponding author. Department of Land, Air & Water Resources, University of California, Davis, Davis, CA, 95616, USA.

E-mail address: smgrodsky@ucdavis.edu (S.M. Grodsky).

¹ Current address: U.S. Fish and Wildlife Service, Pacific Southwest Region, 3020 State University Drive East, Sacramento, CA 95819, USA.



Fig. 1. (A) A black-tailed jackrabbit (*Lepus californicus*) consuming Mojave milkweed (*Asclepias nyctaginifolia*) containing cardenolides in the Ivanpah Valley, Mojave Desert, California, USA. The screenshot was taken from video footage of the first conclusive documentation of Mojave milkweed herbivory by the black-tailed jackrabbit, 1722 h–1729 h, 5 May 2017. (B) Queen butterfly (*Danaus gilippus*) eating a leaf of Mojave milkweed in the Ivanpah Valley, Mojave Desert, California, USA. Along with monarch butterflies (*Danaus plexippus*), queen butterflies use Mojave milkweed as a host plant and sequester cardenolides from the milkweed species for predator defense. Photo credit: Steve Grodsky.

P450 enzymes that metabolize toxins of both woody perennial and herbaceous plants (Ohnishi et al., 2009).

Mojave milkweed (*Asclepias nyctaginifolia*, Apocynaceae) is a rare, perennial desert species of milkweed sporadically distributed in the southwestern United States (Fig. 1). The plant has broad, oval to lance-shaped and thick, fleshy leaves. We observed pubescent Mojave milkweed leaves in the field (S. M. Grodsky, pers. obs.); however, a previous study described leaves grown from seed in a sphagnum peat moss-based soil as glabrous (Agrawal et al., 2009). Agrawal et al. (2009) measured phytochemical concentrations in 24 milkweed species distributed throughout the United States; they determined that Mojave milkweed has high concentrations of cardenolides, quercetin glycosides, and total phenolics relative to northern and eastern *Asclepias* species. Milkweed species sympatric with Mojave milkweed (e.g., *A. asperula*, *A. californica*) also exhibited above average phytochemical concentrations, indicating that aridland *Asclepias* species may have adapted more potent chemical defenses in resource limited environments (Agrawal et al., 2009). However, phytochemical concentrations may vary within populations of a given milkweed species (Panter et al., 2012). Studies on the effects of any milkweed phytochemicals, including those of Mojave milkweed, on the black-tailed jackrabbit are absent from the peer-reviewed literature.

On 5 May 2017, we observed a black-tailed jackrabbit consuming plant material from Mojave milkweed (*Asclepias nyctaginifolia*) in the Ivanpah Valley within the Mojave Desert of California. We documented this herbivory event from continuous video footage recorded using solar-powered cameras deployed to document real-time ecological interactions at select Mojave milkweed locations in the Ivanpah Valley. The black-tailed jackrabbit fed on the milkweed plant for a period of ~7 min (1722 h–1729 h), during which time it consumed 16 of the 21 (76%) leaves comprising the aboveground biomass of the milkweed. We noted exudation of latex from the milkweed early during the herbivory event, but this chemical defense did not deter the jackrabbit from subsequent feeding on the plant. The black-tailed jackrabbit appeared to select leaves to eat after smelling individual leaves; it fed on leaves of the milkweed by biting off stems of leaves near the base of the plant. The black-tailed jackrabbit consumed each leaf entirely, leaving no part of a leaf it had begun eating unconsumed. The black-tailed jackrabbit primarily focused its foraging on leaves of the milkweed, occasionally consuming parts of stems.

Supplementary video related to this article can be found at <https://doi.org/10.1016/j.jaridenv.2019.103991>.

During a concurrent study, we measured the Mojave milkweed plant used by the black-tailed jackrabbit three days prior the herbivory event (2 May 2017); the plant was non-reproductive and had a total volume of 21.59 cm³ (Fig. 1A). On 15 May 2017, we returned to the site of the

herbivory event and measured Mojave milkweed plants in the area. We recorded that the plant partially eaten by the black-tailed jackrabbit during the herbivory event and another non-reproductive Mojave milkweed plant within 1 m were no longer present aboveground; it was unclear whether black-tailed jackrabbits consumed all leaves and stems of these individuals or if remaining plant material was removed by other herbivores. Two large, reproductive Mojave milkweed plants (volume = 86.36 cm³ and 116.84 cm³, respectively) < 3 m from these juveniles showed no signs of herbivory.

Consumption of Mojave milkweed by the black-tailed jackrabbit during spring in the Mojave Desert elicits novel insights into the nutritional ecology of this hare species. The black-tailed jackrabbit consumed Mojave milkweed leaves with high phytochemical concentrations, thus it also may exploit other milkweed species in aridland plant communities with similarly potent chemical defenses. In 2017, the Ivanpah Valley received 10 cm of winter and spring rains, resulting in abundant and diverse grasses and forbs during the growing season (S. M. Grodsky, pers. obs.). Despite the high availability of grasses (e.g., *Bromus madritensis*, *Hilaria rigida*) and forbs (e.g., *Chaenactis fremontii*, *Sphaeralcea ambigua*), the jackrabbit selected to feed on Mojave milkweed containing phytochemicals. Foraging theory suggests that the black-tailed jackrabbit consumes a more variable diet in spring, which limits intake of any one plant compound (Meyer and Karasov, 1991). Additionally, black-tailed jackrabbits may therapeutically exploit plant secondary compounds for defense against parasites and pathogens, driving the species to select a varied diet that includes plants rich in plant secondary compounds (Forbey and Hunter, 2012). The potential nutritional and therapeutic qualities of Mojave milkweed plants consumed by the black-tailed jackrabbit in moderation and with a varied diet may have overrode any negative physiological consequences from ingesting plant secondary compounds, such as diuresis (Dearing et al., 2002). In arid environments, cardenolide concentrations in leaves and latex of *Asclepias eriocarpa* increased throughout the growing season (Malcolm, 1991). Mojave milkweed may exhibit the same temporal increase in cardenolide content as plants grow, which may explain why the black-tailed jackrabbit ate young, non-reproductive milkweed plants and avoided older, reproductive milkweed plants. In contrast, black-tailed jackrabbits discard young leaves of desert perennials like creosote (*Larrea tridentata*) because these plant parts contain large amounts of unpalatable phenolic compounds (Nagy et al., 1976).

Given the occurrence of the black-tailed jackrabbit and rarity of Mojave milkweed in the Ivanpah Valley (S. M. Grodsky, pers. obs.), black-tailed jackrabbit herbivory may present potential conservation issues for Mojave milkweed. Mojave milkweed occurs in small, widely spaced populations in shallow washes throughout the eastern Mojave Desert. Its limited range in California has led to its designation as

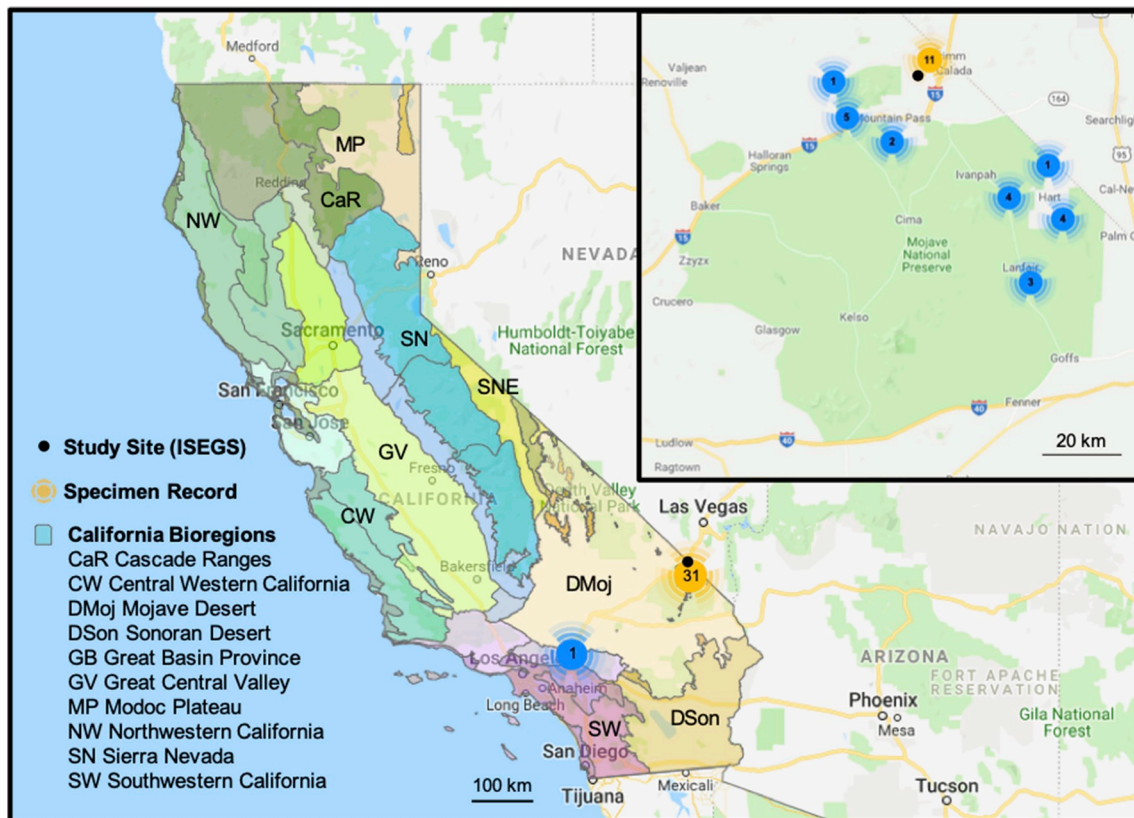


Fig. 2. Map illustrating the restricted range of Mojave milkweed (*Aclepias nyctaginifolia*) in California (CA), USA. The location of Ivanpah Solar Electric Generating System (ISEGS) within the Ivanpah Valley, Nipton, CA, USA and California Bioregions based on The Jepson Manual (Baldwin et al., 2012) are denoted on the map. Specimen records for Mojave milkweed from the Consortium of California Herbaria One are represented by blue circles (< 10 records) and yellow circles (> 10 records). Numbers within circles represent number of specimen records for a specific location. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

“seriously endangered in California” by the California Native Plant Society (Fig. 2). Mojave milkweed is seasonally iteroparous, emerging in both spring and fall from underground tubers, and it reproduces only when soil moisture is sufficient for fruit production (Moore and Andre, 2014). Considering the strict environmental conditions required for Mojave milkweed reproduction, black-tailed jackrabbit herbivory may limit reproduction of the milkweed species. In a concurrent study, we surveyed Mojave milkweed during spring and fall in the Ivanpah Valley from 2017 through fall 2019, and most milkweed plants in spring were completely eaten prior to setting fruit (e.g., during flowering), even in the wettest spring growing season. However, we also observed that many of the same Mojave milkweed plants experienced limited herbivory and set fruit in fall (S. M. Grodsky, pers. obs.), potentially indicating that black-tailed jackrabbits shifted their diet from herbaceous plants to woody perennials in fall, as suggested by previous dietary studies (Meyer and Karasov, 1991).

Use of Mojave milkweed by the black-tailed jackrabbit may affect the critically endangered monarch butterfly (*Danaus plexippus*) and its close relative the queen butterfly (*Danaus gilippus*) in arid environments. Our concurrent field studies in the Ivanpah Valley have verified that both the monarch and queen butterfly (Fig. 1B) use Mojave milkweed as a host plant. The western population of migratory monarch butterflies has declined in number by 86% from 2017 to 2019 and by 99.4% from 1980 to 2019, respectively (The Xerces Society for Invertebrate Conservation, 2019). The monarch butterfly will soon be considered for federal protection under the United States Endangered Species Act. The tritrophic interaction between *Danaus* species and milkweed involving aposematic coloration, sequestration of toxic cardenolides from milkweed host plants, and subsequent defense against predators is a well-documented paradigm in chemical ecology (Agrawal et al., 2012). Our

results demonstrate that the black-tailed jackrabbit can tolerate the cardenolide concentrations found in a western *Asclepias* species also used by monarch and queen butterflies as host plants. Therefore, competition for limited milkweed resources may occur between the black-tailed jackrabbit, a fecund and formidable herbivore, and monarch and queen butterflies in arid environments. For example, lack of availability of Mojave milkweed caused by black-tailed jackrabbit herbivory may limit oviposition sites for monarch and queen butterflies. Conversely, black-tailed jackrabbit herbivory may induce regeneration of younger vegetative stems of Mojave milkweed, and several studies suggest that the monarch butterfly prefers to oviposit on young stems of milkweed (Alcock et al., 2016; Haan and Landis, 2019).

Anthropogenic land-use and land-cover change in the western United States may exacerbate negative ecological consequences of Mojave milkweed herbivory by the black-tailed jackrabbit. Disturbance associated with anthropogenic activity typically favors “generalist” species over “specialist” species. Disturbances in desert ecosystems, including energy development, off-highway vehicle use, agriculture, and urbanization, are likely to benefit habitat generalists like the black-tailed jackrabbit, whereas Mojave milkweed is an endemic desert specialist maladapted to disturbance and thereby may be negatively affected by human activities (Moore-O’Leary et al., 2017). Given the toxicity of milkweed species to domestic livestock (e.g., Malcolm, 1991), overgrazing in arid environments may induce increased black-tailed jackrabbit herbivory on Mojave milkweed via reduction in availability of other forbs and grasses combined with avoidance of milkweed species by livestock.

Utility-scale solar energy development, along with other anthropogenic disturbances, in arid environments can fragment protected wildlife areas and their hydrological resources, which may, in turn,

negatively affect Mojave milkweed and alter herbivore-plant relationships in desert ecosystems (Hernandez et al., 2015). Further, solar energy development in deserts may affect ecological interfaces between soils, Mojave milkweed, and herbivores by altering and disturbing habitat, thereby affecting species-species and species-process interactions among Mojave milkweed, the black-tailed jackrabbit, and monarch and queen butterflies (Grodsky et al., 2017). Cardenolide content in milkweed species decreases in response to increased water stress and shade (Agrawal et al., 2012); thus, microhabitat alterations from solar arrays and heliostats that potentially change hydrology and light availability may reduce cardenolide concentrations in Mojave milkweed, making this milkweed species more susceptible to herbivory from the black-tailed jackrabbit and other desert herbivores. Fencing around solar facilities excludes herbivores that compete with the black-tailed jackrabbit for plant resources, including the wild burro (*Equus asinus*) and the Mojave desert tortoise (*Gopherus agassizii*), which may lead to locally increased black-tailed jackrabbit abundance and thereby potentially increased herbivory on Mojave milkweed and competition with monarch and queen butterflies for Mojave milkweed resources inside solar facilities.

Observations of vertebrate foraging behavior is required to better determine how wild herbivores perceive phytochemical-bearing milkweed (Malcolm, 1991), yet such observations are difficult to make in the field and virtually absent from the literature. Our use of remote, solar-powered video cameras allowed us to record the first conclusive evidence that the black-tailed jackrabbit consumes Mojave milkweed containing phytochemicals in the Mojave Desert of California. We suggest that future studies employ remote video cameras or camera traps at milkweed locations in arid environments, in addition to locations of other plants of conservation concern, to capture evidence of herbivory *in situ* for a variety of milkweed and aridland species. Black-tailed jackrabbit herbivory on Mojave milkweed may have negative ecological effects on rare Mojave milkweed and critically endangered monarch butterflies in California, and these negative effects may be exacerbated by anthropogenic disturbance in desert ecosystems.

Our ecological observations illustrate the complex interactions potentially affected by disturbance from commercial development of solar energy in the Mojave Desert. Siting solar energy facilities in marginalized landscapes such as contaminated and salt-affected agricultural lands to create a techno-ecological synergy (TES) rather than in undeveloped desert ecosystems can alleviate negative ecological consequences of solar energy development (Hoffacker et al., 2017). In contrast to use of undeveloped environments for solar energy development, TESs of solar energy produce outcomes favorable for both technological systems (e.g., photovoltaic module efficiency) and ecological systems (e.g., ecological restoration, land-sparing) (Hernandez et al., 2019). Decision-making and policy related to solar energy development in desert ecosystems informed by research that considers technological opportunities as well as potential ecological effects on native desert species and multi-species, ecological relationships (e.g., “bottom-up” interactions) is essential to optimize solar energy-TES outcomes (Grodsky et al., 2017; Moore-O’Leary et al., 2017, Hernandez et al., 2019).

Acknowledgments

Our research was funded by the California Energy Commission (Electric Program Investment Charge-15-060) and the Department of Land, Air & Water Resources at the University of California, Davis. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

References

- Agrawal, A.A., Fishbein, M., 2006. Plant defense syndromes. *Ecology* 87, S132–S149.
- Agrawal, A.A., Fishbein, M., Jetter, R., Salminen, J., Goldstein, J.B., Freitag, A.E., Sparks, J.P., 2009. Phylogenetic ecology of leaf surface traits in the milkweeds (*Asclepias* spp.): chemistry, ecophysiology, and insect behavior. *New Phytol.* 183, 848–867.
- Agrawal, A.A., Petschenka, G., Bingham, R.A., Weber, M.G., Rasmann, S., 2012. Toxic cardenolides: chemical ecology and coevolution of specialized plant-herbivore interactions. *New Phytol.* 194, 28–45.
- Alcock, J., Brower, L.P., Williams, E.H., 2016. Monarch butterflies use regenerating milkweeds for reproduction in mowed hayfields in northern Virginia. *J. Lepid. Soc.* 70, 177–181.
- Baldwin, B., Goldman, D., Keil, D., Patterson, R., Rosatti, T., Wilken, D., 2012. *The Jepson Manual: Vascular Plants of California*, second ed. University of California Press, Berkeley.
- Cates, R.G., Rhoades, D.F., 1977. Patterns in the production of antiherbivore chemical defenses in plant communities. *Biochem. Syst. Ecol.* 5, 185–193.
- Coley, P.D., Bryant, J.P., Chapin III, F.S., 1985. Resource availability and plant anti-herbivore defense. *Science* 230, 895–899.
- Chew, R.M., Chew, A.E., 1970. Energy relationships of the mammals of a desert scrub (*Larrea tridentata*) community. *Ecol. Monogr.* 40, 1–21.
- Currie, P.O., Goodwin, D.L., 1966. Consumption of forage by black-tailed jackrabbits on salt-desert ranges of Utah. *J. Wildl. Manag.* 30, 304.
- Dearing, D.M., Mangione, A.M., Karasov, W.H., 2002. Ingestion of plant secondary compounds cause diuresis in desert herbivores. *Oecologia* 130, 576–584.
- Forbey, J.S., Hunter, M.D., 2012. The herbivore’s prescription: a pharm-ecological perspective on host-plant use by vertebrate and invertebrate herbivores. In: Iason, G.R., Dicke, M., Hartley, S.E. (Eds.), *The Ecology of Plant Secondary Metabolites: from Genes to Global Processes*. Cambridge University Press, New York, pp. 78–100.
- Grodsky, S.M., Moore-O’Leary, K.A., Hernandez, R.R., 2017. From butterflies to bighorns: multi-dimensional species-species and species-process interactions may inform sustainable solar energy development in desert ecosystems. In: Reynolds, R.L. (Ed.), *Proceedings of the 31st Annual Desert Symposium*. California State University Desert Studies Center, Zzyzx, CA, pp. 322–327.
- Haan, N.L., Landis, D.A., 2019. Grassland disturbance increases monarch butterfly oviposition and decreases arthropod predator abundance. *Biol. Conserv.* 233, 185–192.
- Hernandez, R.R., Hoffacker, M.K., Murphy-Mariscal, M.L., Wu, G.C., Allen, M.F., 2015. Solar energy development impacts on land cover change and protected areas. *Proc. Natl. Acad. Sci. Unit. States Am.* 112, 13579–13584.
- Hernandez, R.R., Armstrong, A., Burney, J., Ryan, G., Moore-O’Leary, K.A., Diedhiou, I., Grodsky, S.M., Saul-Gershenz, L., Davis, R., Macnick, J., Mulvaney, D., Heath, G.A., Easter, S.B., Hoffacker, M.K., Allen, M.F., Kammen, D.M., 2019. Techno-ecological synergies of solar energy produce beneficial outcomes across industrial-ecological boundaries to mitigate global environmental change. *Nat. Sustain.* <https://doi.org/10.1038/s41893-019-0309-z>. in press.
- Hayden, P., 1966. Food habits of black-tailed jackrabbits in southern Nevada. *J. Mammal.* 47, 42–46.
- Hoffacker, M.K., Allen, M.F., Hernandez, R.R., 2017. Land sparing opportunities for solar energy development in agricultural landscapes: a case study of the Great Central Valley, CA, USA. *Environ. Sci. Technol.* 51, 14472–14482.
- Huitu, O., Forbes, K.M., Helander, M., Julkunen-Tiitto, R., Lambin, X., Saikkonen, K., Stuart, P., Sulkama, S., Hartley, S., 2014. Silicon, endophytes and secondary metabolites as grass defenses against mammalian herbivores. *Front. Plant Sci.* 5, 1–10.
- Malcolm, S.B., 1991. Cardenolide-mediated interactions between plants and herbivores. In: Rosenthal, G.A., Berenbaum, M.R. (Eds.), *Herbivores: Their Interactions with Plant Secondary Metabolites*, second ed. Academic Press, San Diego, California.
- Meyer, M.W., Karasov, W.H., 1991. Chemical aspects of herbivory in arid and semiarid habitats. In: Palo, R.T., Robbins, C.T. (Eds.), *Plant Defenses against Mammalian Herbivory*. CRC Press, Boca Raton, FL, pp. 167–187.
- Moore, K.A., Andre, J.M., 2014. Rare plant diversity in the California deserts: priorities for research and conservation. *Fremontia* 42, 9–14.
- Moore-O’Leary, K.A., Hernandez, R.R., Abella, S., Johnston, D., Kreidler, J., Swanson, A., Lovich, K., 2017. Sustainability of utility-scale solar energy-critical ecological concepts. *Front. Ecol. Environ.* 15, 385–394.
- Nagy, K.A., Shoemaker, V.H., Costa, W.R., 1976. Water, electrolyte, and nitrogen budgets of jackrabbits (*Lepus californicus*). *Physiol. Zool.* 49, 351–363.
- Ohnishi, T., Yokota, T., Mizutani, M., 2009. Insights into the function and evolution of P450s in plant steroid metabolism. *Phytochemistry* 70, 1918–1929.
- Panter, K.E., Welch, K.D., Gardener, D.R., Lee, S.T., Green, B.T., Pfister, J.A., Cook, D., Davis, T.Z., Stegelmeier, B.L., 2012. Poisonous plants of the United States. In: Gupta, R.C. (Ed.), *Veterinary Toxicology*. Academic Press, Oxford, pp. 1029–1079.
- Simes, M.T., Longshore, K.M., Nussear, K.E., Beatty, G.L., Brown, D.E., Esque, T.C., 2015. Black-tailed and white-tailed jackrabbits in the American West: history, ecology, ecological significance, and survey methods. *West. N. Am. Nat.* 75, 491–519.
- The Xerces Society for Invertebrate Conservation, 2019. Record low number of overwintering monarch butterflies in California. Available at: <https://xerces.org/2019/01/17/record-low-overwintering-monarchs-in-california/>, Accessed date: 27 February 2019.