Western North American Naturalist 86(2), © 2026, pp. 349–365

D. Carl Freeman (1951–2024): Extraordinary Scientist with a Passion for Data Sets

Fig. 1. Carl Freeman at the Salt Creek big sagebrush hybrid zone, Utah, in 2004.

Dwight Carl Freeman (Fig. 1), known as Carl among friends and collaborators, was born on 7 March 1951 in Salt Lake City, Utah, to Dwight Carl Freeman (1922–2003) and Mary Loenza Wassom (1924–2017). He was named after his father but never used the appellation "Junior," preferring to be referenced as D. Carl Freeman in contrast to his father's Dwight C. or Dwight Carl. He was the eldest son with an older sister and two younger brothers. Carl attended public schools in Bountiful, Utah, including Viewmont High School, from which he graduated in 1969. During this time, he was involved in academic and sports activities with a special interest in biology.

Following high school, Freeman enrolled at the University of Utah and majored in biology. This is where he met his two main science mentors, ecological botanists Lionel G. Klikoff (1937–2016) and Kimball T. Harper (1931–2011). As he transitioned from an undergraduate to a master's degree student, Freeman worked on desert ecology projects (Klikoff and Freeman 1974, Klikoff et al. 1975).[1] Freeman received a B.S. in Biology in 1973. About this time, Dr. Klikoff introduced Freeman to the chemist Henry Erying (1901–1981), who served as dean of the University of Utah graduate school and chair of the Chemistry Department. A much-honored scientist and a member of the National Academy of Sciences, Eyring was a one-time colleague of Albert Einstein at Princeton University (Eyring 2007). Eyring asked Freeman to collaborate on a test population of the Eyring–Stover Survival Theory Model, which explores the effects of predation, competition, aging, and community dynamics using data from buttercup (*Ranunculus*), elm (*Ulmus*), and hawthorn (*Crataegus*) populations. The resulting research paper was published in the prestigious Proceedings of the National Academy of Sciences (Freeman et al. 1974). Freeman then started his master's program at the University of Utah. However, since his mentors moved to other institutions (Dr. Klikoff assuming the chairmanship of the Biology Department at Allegany College in Meadville, Pennsylvania, and Dr. Harper becoming chair of the Brigham Young University Department of Botany and Range Science), Freeman decided to follow Dr. Harper to Brigham Young University (BYU). This move did not slow him down. He completed his master's degree project on resource utilization by the sexes of dioecious plants in 1976 and saw it published the same year in *Science* (Freeman et al. 1976). These activities cemented Freeman's reputation as a scientist.

[1]In-text citations for which D.C. Freeman is a coauthor are listed in Appendix 1.

Table 1. Summary of Freeman and colleagues' research on sex expression in plants.

Plant taxa	Description of research	References
Many species	Evolution, ecology, variability and spatial distribution of dioecious plants	El-Keblawy and Freeman 1999; Freeman 1976, 1977; Freeman et al. 1976, 1979, 1997, 2007; Golenberg and Freeman 2006; Sinclair et al. 2009, 2012, 2013a, 2013b
Many species	Evolution, ecology, variability and spatial distribution of monoecious plants	Bickel and Freeman 1993; Freeman et al. 1981
Several species	Sex switching and flexibility	Barker et al. 1980; Freeman et al. 1979, 1982
Several species	Sex expression as effected by stress, competition, and/or flowering	Freeman and Harper 1980; Freeman and McArthur 1982, 1984; Sinclair et al. 2009
Atriplex canescens	Sex expression, genetics, flowering, physiology, distribution, seed orchard technology, pollen flow	Freeman and McArthur 1989; Freeman et al. 1984, 1993c, 1993d, 1994; McArthur and Freeman 1982; McArthur et al. 1978, 1986, 1992; Pendleton et al. 1992, 1994; Tiedemann et al. 1987
Grayia brandegeei	Heterodichogamous gender dynamics	Pendleton et al. 1988, 2000
Spinacia oleracea	Environmental effects, physiology, and sex ratios	Freeman and Vitale 1985; Freeman et al. 1994; Miglia et al. 1996; Vitale and Freeman 1985, 1986; Vitale et al. 1987

It was about that time when E.D. McArthur met Freeman. McArthur was an adjunct faculty member of the BYU Botany and Range Science Department and had been working on sex expression in the dioecious shrub *Atriplex canescens* (fourwing saltbush) as it is influenced by environment (McArthur 1977). For his PhD work, Freeman expanded his master's degree work along similar lines by examining an array of dioecious plant species, including saltbushes (Freeman 1977). McArthur was therefore a natural fit as an advisor on Freeman's doctoral committee. The two of them became fast friends, and with several colleagues they began examining the relationships between genetics and environment in the floral sex expression of dioecious and monoecious plants (McArthur et al. 1978, Freeman et al. 1981, 1984, Freeman and McArthur 1982, 1984, McArthur and Freeman 1982). Freeman became a seasonal employee at the USDA Forest Service's Shrub Sciences Laboratory, McArthur's institutional home on the BYU campus. Eventually, Freeman's search for a permanent academic home garnered an invitation for an interview in the Department of Biological Sciences of Wayne State University (WSU), Detroit, Michigan. This resulted in his being hired as an assistant professor in 1977. Freeman continued as a summer seasonal employee for a few years at the Shrub Sciences Laboratory in Provo. Also while at BYU, Freeman became a family man, marrying Loralee White. Their family in time expanded to include five adopted children: Douglas, Steven, Marissa, and twins Alisha and Rebecca, who all joined the family in the Detroit area.

Focus on Plant Sex Expression

Expanding his research of the genetic and environmental influences on sex expression in dioecious and monoecious plants and solidifying his research credentials at Wayne State University, Freeman, in collaboration with McArthur, prepared and submitted a research proposal, "The Adaptive Significance of Sex Change in Plants," to the Population and Physiological Program of the National Science Foundation. This proposal was funded for $105,000 (1981–1984). The research stimulated by this grant led to many productive and informative studies continuing over more than three decades involving several WSU graduate students (Kathy Miglia, Burton Pendleton, Rosemary Pendleton, Jordan Sinclair, and Jeffrey Vitale) and numerous colleagues. Freeman and his colleagues continued research on sex expression in plants throughout his career (Table 1).

Focus on Hybrid Zones

As Freeman was establishing his credentials at Wayne State University as a teacher and researcher, he interacted with Dr. William Moore and his postdoctoral associate Dr. John Graham, who were working in the neighboring lab. Moore

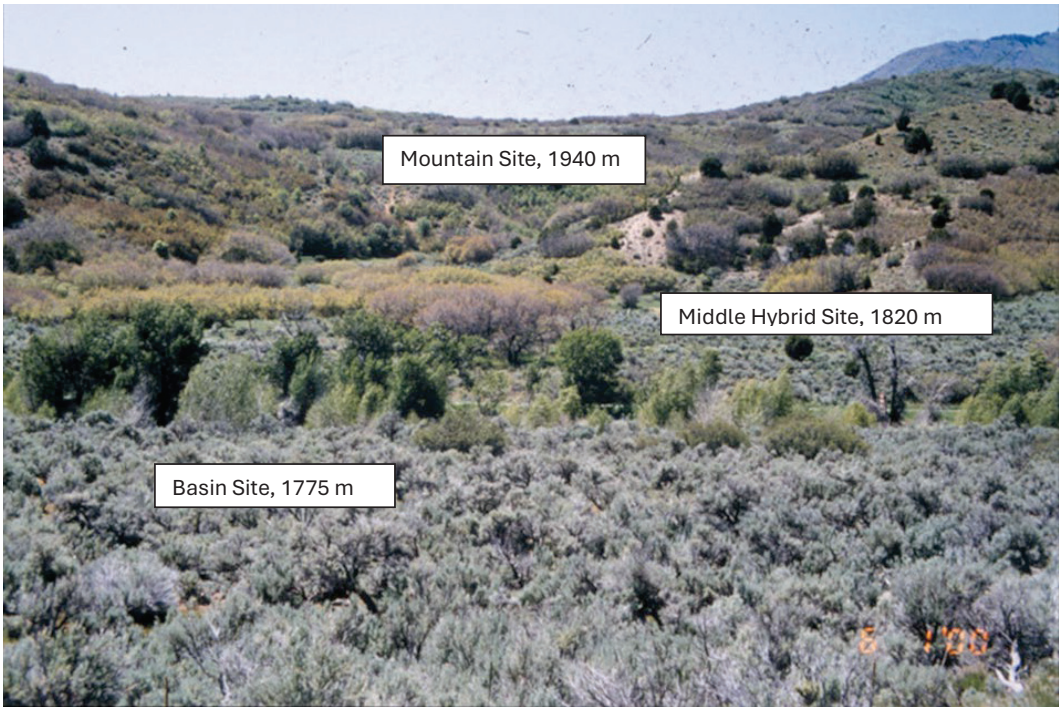

Fig. 2. Salt Creek big sagebrush hybrid zone, Utah, 2000.

and Graham were studying mtDNA variation across hybrid zones in woodpeckers (three subspecies of Northern Flicker [*Colaptes auratus*]). At the time, stable hybrid zones were seen as a problem for prevailing theories of speciation (Moore 1977, Barton and Hewitt 1985, Harrison 1990). Durant McArthur was simultaneously working on hybridization in big sagebrush (*Artemisia tridentata*) and its relatives, the subgenus *Tridentatae* of *Artemisia* (McArthur et al. 1979, 1988). Moore's work was with birds, and the tests of hybrid zone theory were indirect. But Freeman and McArthur saw the ultimate possibility of directly testing hybrid zone theory by using the big sagebrush hybrid as a model system. To that end they set up a series of studies on narrow hybrid zones at the interface of distributions of basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*). These studies examined distinguishing characteristics of parental and putative hybrid or introgressed plants in a narrow hybrid zone (Table 2), culminating in a reciprocal transplant experiment in the Salt Creek Hybrid Zone.

A series of studies over multiple sagebrush hybrid zones, but concentrating on the Salt Creek Hybrid zone (Fig. 2), focused on plant morphology, hybrid selection and fitness, developmental instability, soil properties, respiration and water potential, distribution of terpenes, insects and galls, root endophytes (mycorrhizae), soil microflora, and genetic markers (Table 2). These studies supported the bounded hybrid superiority model of Moore (1977) over other proposed stable hybrid zone models (Harrison 1993). The main finding was that hybrids exhibited greater fitness than the parental subspecies but only in the hybrid zone. A final discovery was that soil mycorrhizae contributed to hybrid superiority in the hybrid zone. Freeman's graduate students David Byrd, Kathy Miglia, and Han Wang contributed to these studies. It is unfortunate that the reciprocal transplant experiment at Salt Creek including all plants and fence infrastructure was completely consumed by a wildfire in July 2007, thus preventing continued studies (Bergreen and Meyers 2007).

Focus on Evolutionary Developmental Biology

Freeman and his colleagues, especially John H. Graham and John M. Emlen (1938–2025), conducted robust research in developmental

TABLE 2. Individual studies or reviews contributing to the big sagebrush (*Artemisia tridentata*) hybrid zone body of knowledge. See Appendix 1 for full citations.

Title	Site	Results and comments	Reference
Natural and artificial hybridization between big sagebrush subspecies	Diamond Fork Canyon, Utah County, UT	Controlled hybridization was shown to be successful through detection and assay of chemical markers. Artificial and natural hybridization success between subspecies *tridentata* and *vaseyana* was demonstrated by analysis of putative hybrid and parental populations. Coumarins, monoterpenoids, and morphological characteristics were analyzed.	McArthur et al. 1988
Narrow hybrid zone between two subspecies of big sagebrush. I. Characterization	Wasatch Mountain Foothills, Orem, Utah County, UT; Salt Creek Canyon, Juab County, UT	Parental taxa were demonstrated to differ in anatomy, morphology, and flavonoid and coumarin content, as well as various growth parameters. Hybrids were determined to be intermediate for the majority of traits examined, including flavonoid and coumarin composition. Multivariate statistics showed that these taxa could be unambiguously identified using simple field measures of morphology. A hybrid index was constructed using principal component analyses on morphological variables.	Freeman et al. 1991
Narrow hybrid zone between two subspecies of big sagebrush. II. Selection gradients and hybrid fitness	Wasatch Mountain Foothills, Orem, Utah County, UT; Salt Creek Canyon, Juab County, UT	Herbivore loads and seed germination data didn't support the dynamic equilibrium hypothesis for the maintenance of stable hybrid zones in either study site.	Graham et al. 1995
Narrow hybrid zone between two subspecies of big sagebrush. III. Developmental instability	Wasatch Mountains Foothills, Orem, Utah County, UT; Salt Creek Canyon, Juab County, UT	An examination of developmental instability using the morphological characteristics of inflorescence length, branch length, relative position of fertile and sterile branches on new stems, leaf length, and distance of the leaf base to the widest portion of the leaf. Results supported the bounded hybrid superiority hypothesis over the dynamic equilibrium hypothesis for maintenance of stable hybrid zones.	Freeman et al. 1995
Narrow hybrid zone between two subspecies of big sagebrush. IV. Reciprocal transplant experiments	Salt Creek Canyon, Juab County, UT	Reciprocal transplant experiments showed significant genotype-by-environment interactions for a number of fitness components, including germination, growth, and reproduction. Hybrids were the most fit within the hybrid garden. In the parental gardens, the native parental taxon was more fit than either the alien parental or hybrids, results consistent with exogenous selection assumptions contained in the bounded hybrid superiority model.	Wang et al. 1997
Narrow hybrid zone between two subspecies of big sagebrush. V. Soil properties	Clear Creek Canyon, Sevier County, UT; Salt Creek Canyon, Juab County, UT	The elemental (Na, Ca, Mg, Mo, and Ba) composition, depth, and pH of soil in the parental habitats differed significantly from one another and from the hybrid zone habitat. The hybrid zone soil was not just a blend of the parental habitat soils but possessed novel characteristics.	Wang et al. 1998
Narrow hybrid zone between two subspecies of big sagebrush. VI. Respiration and water potential	Salt Creek Canyon, Juab County, UT	Respiration and stem water potential (ψ) were examined in parental and hybrid big sagebrush grown in common gardens within each parental zone and in the hybrid zone. Plants were sampled in July, August, and September, i.e., immediately before, during, and after flowering. The habitats differed from one another, and there were significant garden-by-date interactions. The source populations also differed significantly from one another, but there were no significant garden-by-source interactions. Hybrid plants had intermediate	McArthur et al. 1998

TABLE 2. Continued.

Title	Site	Results and comments	Reference
		respiration rates and did not suffer greater water stress than parental plants. Hybrid plants showed no apparent decrease in adaptation in the important physiological traits of respiration and water stress in the hybrid zone.	
Narrow hybrid zone between two subspecies of big sagebrush. VII. Community and demographic research	Clear Creek Canyon, Sevier County, UT	An examination of the floristic and vegetative composition of the communities inhabited by basin big sagebrush and mountain big sagebrush and their hybrids as well as the demographic structure of the sagebrush populations in their native habitats showed that species composition differed among the parental sites and the hybrid zone. The two big sagebrush subspecies and their hybrids were each associated with different groups of species, and occupied edaphically distinct habitats.	Freeman et al. 1999c
Narrow hybrid zone between two subspecies of big sagebrush. VIII. Spatial and temporal pattern of terpenes	Salt Creek Canyon, Juab County, UT	Parental and hybrid populations of big sagebrush varied in terpene composition across the hybrid zone. Terpenes differed between seasons, subspecies (including hybrids), individual plants, and leaves from vegetative branches and inflorescences on the same plant. While hybrids were intermediate for most common terpenes, several terpenes produced by both parental taxa were not produced by hybrids. Furthermore, hybrids produced novel terpenes. The clinal variation of terpenes was highly correlated with both morphological variation and edaphic gradients.	Byrd et al. 1999
Narrow hybrid zone between two subspecies of big sagebrush. IX. Elemental uptake and niche separation	Salt Creek Canyon, Juab County, UT	The concentrations of selected elements and their biological absorption coefficients were determined for leaves from sagebrush in native stands and reciprocal transplant gardens to determine whether niche differentiation occurs among the parental taxa and their hybrids in the big sagebrush hybrid zone. Concentrations of elements differed significantly between the subspecies and their hybrids, with significant genotype-by-environment interactions observed for several essential elements. Observed niche differentiation provided support for the bounded hybrid superiority model as big sagebrush parental taxa and their hybrids were adapted to their respective unique habitats.	Wang et al. 1999
Ecotones: introduction, scale, and big sagebrush example	North America, in general; Salt Creek Canyon, Juab County, UT	Hybridization in general often occurs at ecotones, the transitions between distinct ecological communities or ecosystems. Members of the big sagebrush complex (subgenus *Tridentate*) often overlap in ecotones affording opportunities for hybridization. A model hybrid zone system based on basin and mountain big sagebrush hybrid zones supports the bounded hybrid superiority hypothesis over competing models.	McArthur and Sanderson 1999
Ecological analysis of the big sagebrush hybrid zone	Diamond Fork Canyon, Utah County, UT; Wasatch Mountain Foothills, Orem, Utah County, UT; Salt Creek Canyon, Juab Co., UT	Data from hybrid fitness, respiration and water potential, developmental stability, herbivory, nutrient uptake, and transplant studies demonstrate the bounded hybrid superiority hypothesis, i.e., hybrids in the hybrid zone exhibit superior fitness compared to the parental taxa in the hybrid zone but not in the parental taxa habitats.	Graham et al. 1999

TABLE 2. Continued.

Title	Site	Results and comments	Reference
Narrow hybrid zone between two subspecies of big sagebrush. X. Performance in reciprocal transplant gardens	Salt Creek Canyon, Juab County, UT	The performance of basin and mountain big sagebrush and their hybrids was examined over 5 years in 3 common gardens. A garden was located within the native stand of each parental taxon and in the center of the hybrid zone (see Fig. 2). The performance of a plant depended upon the garden in which it was raised and the source population from which it was derived. Different years seemed to favor different taxa. The results were consistent with the bounded hybrid superiority model.	Freeman et al. 1999b
Differences in temperature dependence of respiration distinguish subspecies and hybrid populations of big sagebrush: nature versus nurture	Salt Creek Canyon, Juab County, UT	Mountain big sagebrush grows at slightly higher elevation and at cooler and drier sites than basin big sagebrush. Natural hybrids between the subspecies can be separated by 85 m in elevation and 1.1 km along a transect between parental subspecies (Fig. 2). Three gardens were established with seedlings from 5 populations (basin, near basin, middle hybrid, near mountain, and mountain) of big sagebrush. Physiological measurements (carbon isotope ratios, chlorophyll *a* florescence, and microcalorimetry) showed that both nature and nurture had an influence on the plants.	Smith et al. 1999
Field trip report: shrubland ecotones	Salt Creek Canyon, Juab County, UT	The field trip featured a stop at the Salt Creek Canyon hybrid zone site where the past and ongoing studies were reviewed and demonstrated. The hybrid zone study is located at Salt Cave Hollow in Salt Creek Canyon, ranging in elevation from 1775 m in the Salt Creek flood plain (basin big sagebrush transplant garden) to 1940 m at the mountain big sagebrush garden, a 1.1-km linear distance (Fig. 2).	McArthur et al. 1999
Use of distance measures to access environmental and genetic variability across sagebrush hybrid zones	Clear Creek Canyon, Sevier County, UT; Salt Creek Canyon, Juab County, UT	Euclidean distance measures were analyzed for spatial variation in soil chemistry, vegetation, and insect communities as well as interplant variability in the production of terpenes, elemental leaf concentrations, and plants' biological adsorption coefficients in parental and hybrid gardens. Spatial variation was greatest in the mountain zone, least in the basin zone, and intermediate in the hybrid zone. In all 3 gardens overall, hybrid plants displayed greater variation than either parental taxon in terms of their leaf elemental chemistry and biological absorption coefficients. However, the variability for all parental and hybrid plants increased when they were raised in alien gardens.	Freeman et al. 2001
Narrow hybrid zone between two subspecies of big sagebrush. XI. Plant–insect interactions in reciprocal transplant gardens	Salt Creek Canyon, Juab County, UT	Only grasshoppers and leafminers appeared to distinguish among hybrid and parental genotypes. Coccids, *Clastoptera*, *Trirhabda*, coleophorid larvae, and lepidopteran leaf miners, in contrast, showed more significant variation among environments. Hybrid plants were not more heavily grazed than parental plants, and the hybrid zone was not a sink for herbivores. Insects varied along the elevational gradient, and few seemed to target particular taxa.	Graham et al. 2001a
Narrow hybrid zone between two subspecies of big sagebrush XII. Plant–insect interactions in reciprocal transplant gardens	Salt Creek Canyon, Juab County, UT	Several forms of gall-forming insects specialize on big sagebrush. Gall density was greatest in the mountain garden and least in the basin garden, with much higher variation in gall density among gardens compared with source populations (parental subspecies, 3 hybrid sources or genotypes). Nevertheless,	Graham et al. 2001b

TABLE 2. Continued.

Title	Site	Results and comments	Reference
		significant genotype–environment interactions were observed for 5 of the 7 kinds of galls examined.	
Stress-induced metabolic differences between populations and subspecies of *Artemisia tridentata* (sagebrush) from a single hillside	Salt Creek Canyon, Juab County, UT	Physiological measurements of carbon isotope ratios, chlorophyll fluorescence, and respiratory heat and CO_2 production showed adaptation to site (basin, mountain, and hybrid plants) of origin. When plants were transplanted to foreign sites, stress was noted. Seasonal changes in temperature promoted metabolic responses to sagebrush that differ with population and garden.	Smith et al. 2002
Developmental instability as an appropriate indicator of plan fitness components	Salt Creek Canyon, Juab County, UT	Measures of developmental instability are extremely sensitive to genetic disturbances. These data allowed for the comparison of developmental instability with a composite measure of fecundity over 5 years as well as comparing developmental instability with fitness components from each of the 5 years.	Tracy et al. 2003
Importance of genotype, soil type and location on the performance of parental and hybrid big sagebrush reciprocal transplants in the gardens of Salt Creek Canyon	Salt Creek Canyon, Juab County, UT	Stability of hybrid zones results from a balance between gene flow and selection. Results from a reciprocal transplant experiment involving the big sagebrush hybrid zone showed that the hybrid and parental genotypes were not adapted to either the soils or location; rather it appears that soil microorganisms are adapted to their location. Results do not support the common assumption of hybrid unfitness.	Miglia et al. 2004
The importance of multiple year fitness in a nine-year reciprocal transplant experiment in the gardens of mountain and basin big sagebrush hybrid zone	Salt Creek Canyon, Juab County, UT	Results showed that ecological selection structures the hybrid zone with hybrids demonstrating greater fitness not only in their native garden but also in the parental gardens in support of the bounded hybrid superiority model. This study shows the importance of long-term measures.	Miglia et al. 2005
Genotype, soil type, and locale effects on reciprocal transplant vigor, endophyte growth, and microbial functional diversity of a narrow sagebrush hybrid zone	Salt Creek Canyon, Juab County, UT	The indigenous hybrids had the greatest fitness when grown in their indigenous location and indigenous soil. Such was not the case for the parental genotypes perhaps because of the disruption of the soil structure when the soils were moved into the trenches in the respective gardens. Gene flow appeared to be asymmetrical because when mountain big sagebrush was the maternal parent of F_1 hybrids in the middle hybrid zone habitat, F_1 hybrids were superiorly more fit than when basin big sagebrush was the maternal parent. The genotypes of associated organisms (herbivores, parasites, and soil microorganisms) are perhaps as important as the sagebrush genotypes.	Miglia et al. 2007
Comparison of respiration and growth characteristics of big sagebrush subspecies and hybrids	Salt Creek Canyon, Juab County, UT	Differences between the respiratory and growth characteristics of the 3 populations (basin, middle hybrid, and mountain big sagebrush) explain the hybrid zone architecture of indigenous populations but do not explain the different respiratory characteristics and survival of the transplants.	Hansen et al. 2008

TABLE 2. Continued.

Title	Site	Results and comments	Reference
Symbiotic regulation of plant growth, development and reproduction	Salt Creek Canyon, Juab County, UT	Indigenous multigenerational hybrids had increased fitness when colonized by *Alternaria* sp. endophytes which enhanced hybrid reproduction by 155% on average but depressed parental reproduction by 80%. It follows that seed dispersed outside of a plant's indigenous habitat will carry the endophyte and reduce the resulting offspring's fitness. This limits gene flow across the hybrid zone and inhibits parental taxa from invading the hybrid zone, or each other's habitat, thus promoting speciation.	Rodriguez et al. 2009

biology focused on developmental stability, fluctuating asymmetry, and other measures of homeostasis. Vladimir Zakharov, a Russian scientist who became a collaborator of Freeman and his colleagues, introduced the ecological monitoring method called *Biotest*, which endeavors to evaluate the health of entire ecological communities, not just individual species. It arose from the purely Russian concept of population phenogenetics, the study of genetic and environmental influences on phenotypic variation within and among populations (Zakharov 1989, Zakharov and Graham 1992, Graham 2021). These studies and others related to developmental instability are summarized in Table 3 and have provided insight into both plant and animal community dynamics under various biotic and abiotic stressors.

Additional Research Interests

The three focal areas emphasized above by no means exhaust Freeman's research interest and output. Another important area of research that Freeman was involved in was desert ecology, a focus instilled by Klikoff and Harper, his first two science mentors. Dr. Klikoff involved Freeman in the US/IBP Desert Biome, a program managed by the Ecology Center of Utah State University (United States International Biological Program 1979). Freeman's master's thesis on differential resource allocation of dioecious plants grew in part out of this effort because many of the desert plants he studied were dioecious or monoecious. Likewise, Kimball Harper completed his master's research at the USDA Forest Service's Desert Experimental Range, hereafter referred to as the DER (Harper 1959, Van Buren et al. 2012, McArthur and Kitchen 2013). This site sparked an interest in Freeman that would last his entire career. Freeman's involvement as a seasonal employee of the USDA Forest Service Intermountain Research Station (now the Rocky Mountain Research Station), the agency responsible for the management and maintenance of the DER, enabled his involvement in research activities there. His work on desert ecology focused on the DER but also facilitated wider desert ecology work that included fruitful collaboration with his colleagues Kimball Harper, John Emlen, Freeman's student Jeff Duda, and others. Freeman found the isolated atmosphere at the DER stimulating not only for research but also for scientific thought and research planning. He therefore took many colleagues and students there, partially supported by funding that he

Table 3. Summary of environmental stress studies of Freeman and colleagues.

Stressor	Site	Study species	Results	Reference
Industrial plant effluents	Odessa Port Plant, USSR (now Ukraine)	Black locust (*Robinia pseudo-acacia*) and field bindweed (*Conovolvulus arvensis*); Goldfish (*Carassius auratus*); Terrestrial land snails (*Cepaea nemoralis*)	Leaf and leaflet asymmetry were greater in the stressed sites as opposed to control sites; goldfish with greatest head and mandible deformities were in wastewater ponds containing industrial effluents as compared to ponds without those effluents; snails with greatest helical asymmetry were those which had been treated with agricultural pesticides.	Emlen et al. 1993, 1998, 2002; Freeman et al. 1993a; Graham et al. 1993a, 1993b
Industrial plant effluents	Novgorod, Russia; Bryansk, Russia; Puget Sound, WA, USA	Ground elder (*Aegopodium podagraria*) and fireweed (*Chamerion angustifolium*)	Asymmetry measures leaf widths, leaf and leaflet lengths, and rachis lengths all declined with distance from the industrial plant.	Freeman et al. 1993b
Industrial effluents	Puget Sound, WA, USA	Rockweed (*Fucus gardneri*)	Asymmetry and fractal dimensions of the dichoto-mously branching fronds were greater in the polluted sites than in the pristine sites.	Freeman et al. 1993b, 1996; Graham et al. 1993a, 1993b; Tracy et al. 1995
Environmental gradation	Salt Creek, UT	Big sagebrush subspecies (*Artemesia tridentata* ssp. *tridentata*, *A. t.* ssp. *vaseyana* and their hybrids)	Significant correlation was shown between leaf asymmetry and fitness of reciprocally transplanted parental stock and hybrids.	Freeman et al. 1996
Grazing geographic differences	Almeria, Spain; Málaga Province, Spain	Yellow broom (*Anthyllis cytisoides* L.); Portuguese germander (*Teucrium lusitanicum*)	Investigations showed that growth responses to grazing were measurable through fractal analysis branch structure, that females of *T. lusitanicum* had higher developmental instability, and that different habitat characteristics (coastal versus inland) can induce differential responses of vegetative and reproductive structures.	Aldos et al. 1998a, 1999
Disturbance gradients (mechanized equipment, troop movements and bivouacs, and fire)	Fort Benning, GA	Several species including dwarf sumac (*Rhus copallinum*), wild sweet potato (*Ipomoea pandurata*), and loblolly pine (*Pinus taeda*)	Little correlation with disturbance except for fire on loblolly pine; in general, individual plant variability, and year-to-year variability in growth and moisture availability made meaningful correlation difficult to assess.	Duda et al. 2003; Freeman et al. 2004a; Graham and Duda 2011; Graham et al. 2004, 2008, 2009

obtained from Earthwatch (Earthwatch Institute 2024). Dozens of undergraduate students participated in data collection and environmental education experiences at the DER. Freeman's desert and general ecology work, including some range management, precipitated several publications (Harper et al. 1978, Freeman et al. 1980, Duda et al. 2003, Freilich et al. 2003, Campbell et al. 2010).

Freeman also made contributions in such wide-ranging fields as plant genetics and systematics (McArthur et al. 1981, 1986), marketing (Kelly et al. 1993, 2006), scientific methodology (Byrd and Freeman 1994, Freeman and Byrd 1994, McGowen et al. 2000, Alados et al. 2005), science education (Ferrereia et al. 2010), and especially in medical evaluations (Placzek et al. 1996, 1997, 1998, 2004, Roubal et al. 1999, 2016, 2018, Malone et al. 2006, Cao et al. 2007, Aiello et al. 2017, Declaire et al. 2017). This latter area grew of special interest to him due to some long-standing orthopedic issues he acquired dating back to high school sports activities. As he received medical treatment, his interest and skill in data analyses prompted him to collaborate with physicians to evaluate treatment procedures utilizing his own treatment results.

Community Service

Freeman was a man of many interests and much curiosity who stood out by putting his analytical skills to use for the good of others. As a member of the Wayne State University Honors Council (a faculty advisory body), Freeman was an untiring and vital resource. The data he produced and presentations he created proved invaluable for highlighting honors program outcomes to university colleagues, which was of particular relevance for the founding in 2008 of the expanded Irvin D. Reid Honors College. Freeman never saw the university campus as a stopping place. On the contrary, he was always looking for ways to engage the larger community. Exemplary legacies include his work coordinating a summer program for Detroit high school students to enhance college preparation, and the launch of the Detroit Fellows Tutoring Project, which placed Honors College students one-on-one with pupils in the Detroit Public Schools. Freeman was dedicated to getting students—not just honors students—out and into the world to do things and make a difference. One example is presented by his efforts on behalf of a collaborative Habitat for Humanity project, in which young people helped build a new house on Detroit's east side. He was likewise tireless in supporting undergraduate research. Freeman was brilliant when it came to figuring out how to turn students into colleagues and collaborators. His leadership had an enduring effect—showing students that simple acts can make a lasting difference through diligent application. And Freeman was a master of that. The man was a wonder.

Mentorship and Impact

Freeman was a superb mentor as highlighted by a university news release on a guest lecture presentation by Dr. Jordan Sinclair (Wayne State University Biological Science News 2023):

> **Dr. Jordan Sinclair presents keynote address at research retreat**
>
> Dr. Jordan Sinclair first intersected with biology at an academic recognition luncheon hosted by the athletic department. Freeman, now an emeritus professor in biological sciences, was invited to attend by another student-athlete. Freeman had the vision to see that this mathematically inclined student had the makings of a first-class ecologist. He offered her a summer position doing fieldwork in the southwestern desert [at the Desert Experimental Range] and the trajectory of her life changed. She started taking biology courses while finishing up an M.A. in mathematics and joined the Ph.D. program in biological sciences, working with Dr. Freeman to probe the ecological implications of skewed sex ratios in plants. Jordan emphasized the value of making interpersonal connections in grad school and meetings. She formed connections with a group of graduate students at a conference and they ended up editing a special issue of the American Journal of Botany – while in graduate school!

Another of his graduate students, J.J. Duda, reflected:

> One of the things I valued most about Freeman was his appreciation for people, particularly his students, and the significance that he placed on our scientific endeavors. The how and why of our work truly mattered to him. Whether it was exploring the symmetry of nature, how energy flowed through ecosystems, medical rehabilitation, or evolutionary botany, he approached life and science with genuine infectious enthusiasm.

Yet another graduate student, Han Wang, currently Professor and Director, Center for Circadian Clocks, Soochow University, Suzhou,

China, honored Freeman by making the long trip, >7000 miles from Suzhou to attend the symposium in honor of Freeman sponsored by the Biological Sciences Department of Wayne State University (Wayne State University Biological Science News 2024).

Former PhD students.—Kathy Miglia, Burton Pendleton, Rosemary Pendleton, Jordan Sinclair, Barbara Wachocki, and Han Wang.

Former MA/MS students.—David Byrd, Jeff Duda, Dan Goldschlag, Leandria Hancock, Philip Hermiz, Sarah Hueni, Craig Kellogg, Robert L. Mara, Joel M. Meloche, Mike Stender, and Jeffrey Vitale.

Teaching and Service

Freeman taught a wide range of biology and ecology classes at Wayne State University. He took on administrative roles as well; for a time he was an associate chair of the Department of Biological Sciences. He served on numerous departmental and university-wide faculty committees. In addition, he, students, and colleagues gave dozens of invited and volunteered presentations, oral and poster, at science conferences locally, regionally, nationally, and internationally, including seminars at various universities and other venues.

He was honored by Wayne State University with the Distinguished Faculty Award (1982), Career Development Award (1986), College of Science Teaching Award (1998), Faculty Service Award (2000), and President's Teaching Award (2003).

Freeman received support for his research activities and interests in service to the community (e.g., water quality, public health, and education issues) from a wide range of sources including the National Science Foundation, Environmental Protection Agency, U.S. Department of Agriculture Forest Service, U.S. Geological Survey, Michigan Department of Environmental Quality, Wayne State University, Michigan Corn Growers, Earthwatch, Department of Defense Strategic Environmental Research and Development Program, and other sources. His activities expanded well beyond those of an inquiring scientist to platonic activities to improve the quality of life for the general citizenry, as exemplified by giving congressional testimony on water quality and helping public teachers quantify success in classrooms. He was a sought-after consultant by other researchers, faculty, local and regional governments, and local, regional, and national governmental and non-governmental agencies.

Personal Life

In the early 2000s, Freeman's first marriage dissolved, but he later met his soulmate, Charlene P. Harris, an educator and administrator in the school district of Troy, Michigan. They were married in 2005 and remained inseparable until his death on 26 April 2024. This marriage added two stepsons to Freeman's family, Aaron and Ryan Harris. One joint project Carl and Charlene took on was the renovation and landscaping of an 1891 colonial revival–style, 2½ story, 5900 ft^2 home sitting on 1.6 acres (Rose 2016).

Freeman was a force of nature who made lasting impacts in science and on his friends, students, family, and colleagues. We the authors of this science obituary are pleased to have crossed paths and trodden trails with him.

Acknowledgments

The authors thank Carl Freeman's graduate students Dr. Kathleen Miglia and Dr. Rosemary L. Pendleton; Dr. Stanley G. Kitchen, retired Scientist-In-Charge of the USDA Forest Service, Rocky Mountain Research Station's Desert Experimental Range; Ashley H. MacKenzie, Data Management Specialist of the USGS Western Fisheries Research Center; and Dr. Freeman's wife, Charlene P. Freeman, for thoughtful input on earlier drafts of this article.

Literature Cited

See Appendix 1 for literature contributed by D. Carl Freeman.

Barton, N.H., and G.M. Hewitt. 1985. Analysis of hybrid zones. Annual Review of Ecology and Systematics 16:11–148.

Bergreen, J., and B.W. Meyers. 2007. Wildfires update: Salt Creek blaze tops 21,300 acres as crews dig in to defend homes. Salt Lake Tribune, 23 July 2007. http://www.sltrib.com/ci_6448730

Earthwatch Institute. 2024. https://en.wikipedia.org/Earthwatch_Institute, [Accessed 8 November 2024].

Eyring, H.J. 2007. Mormon Scientist, the life and faith of Henry Eyring. Deseret Book, SLC, UT. 330 pp.

Graham, J.H. 2021. Nature, nurture, and noise: developmental instability, fluctuating asymmetry, and the causes of phenotypic variation. Symmetry 13:1204

Hansen, L.D., L.K. Farnsworth, N.K. Itoga, A. Nicholson, H.L. Summers, M.C. Whitsitt, and E.D. McArthur. 2008. Two subspecies and a hybrid of big sagebrush: a comparison of respiration and growth characteristics. Journal of Arid Environments 72:643–651.

Harper, K.T. 1959. Vegetational changes in a shadscale-winterfat plant association during twenty-three years of controlled grazing. Master's thesis, Brigham Young University, Provo, UT. 68 pp.

Harrison, R.G. 1990. Hybrid zones: windows on evolutionary processes, Oxford Surveys in Evolutionary Biology 7:69–128.

Harrison, R.G., editor. 1993. Hybrid zones and the evolutionary process. Oxford University Press, New York, NY. 364 pp.

McArthur, E.D. 1977. Environmentally induced changes of sex expression in *Atriplex canescens*. Heredity 38:97–103.

McArthur, E.D., A.C. Blauer, A.P. Plummer, and R. Stevens. 1979. Characteristics and hybridization of important Intermountain shrubs. III. Sunflower family. USDA Forest Service. Intermountain Forest and Range Experiment Station, Ogden UT. Research Paper INT-220. 82 pp.

McArthur, E.D., and S.G. Kitchen. 2013. Desert Experimental Range: annotated bibliography. USDA Forest Service Rocky Mountain Research Station, Fort Collins, CO. General Technical Report RMRS-GTR-312WWW. 52 pp.

McArthur, E.D., S.B. Monsen, and R. Stevens. 1999. Field trip report: shrubland ecotones. Pages 293–299 in E.D. McArthur, W.K. Ostler, and C.L. Wambolt, compilers, Proceedings; shrubland ecotones. 12–14 August 1998, Ephraim, UT. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station Proceedings RMRS-P-11, Ogden, UT. 299 pp.

McArthur, E.D., B.L. Welch, and S.C. Sanderson. 1988. Natural and artificial hybridization between big sagebrush (*Artemisia tridentata*) subspecies. Journal of Heredity 79:268–276.

McArthur, E.D. and S.C. Sanderson. 1999. Ecotones: Introduction, scale, and big sagebrush example. Pages 3–8 *in* E.D. McArthur, W.K. Ostler, and C.L. Wambolt, compilers, Proceedings: shrubland ecotones; 12–14 August 1998, Ephraim, UT. Proceedings RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 299 pp.

Moore, W.S. 1977. An evaluation of narrow hybrid zones in vertebrates. Quarterly Review of Biology 52:263–277.

Rose, J. 2016. Historic Troy house had lavish work done on building and grounds. Detroit Free Press, November 26, 2016.

United States International Biological Program. 1979. Final progress reports. U.S. International Biological Program, Desert Biome, Utah State University, Logan, UT. 8 pp.

Van Buren, R., L. Allphin, and M. Philbrik. 2012. Obituary; Kimball Taylor Harper, 1931–2011. Western North American Naturalist 72: 112–117.

Wayne State University Biological Sciences News. 2023. A chaotic trajectory: Math, biology and agriculture, 10 February 2023. Wayne State University, College of Liberal Arts and Sciences, Biological Sciences, Detroit, MI. 1 p.

Wayne State University Biological Sciences News. 2024. Carl Freeman Memorial Symposium draws colleagues and mentees from faraway places. 17 October 2024. Wayne State University, College of Liberal Arts and Sciences, Biological Sciences, Detroit, MI. 1 p.

Zakharov, V.M. 1989. Future prospects for population phenogenetics. Soviet Scientific Reviews Book Series, Section F Physiology and General Biology Reviews 4:1–79.

Zakharov V.M., and J.H. Graham. 1992. Developmental stability in natural populations. Acta Zoologica Fennica. 191:1–200.

E. Durant McArthur

Scientist Emeritus, Rocky Mountain Research Station, USDA Forest Service, St. George, UT 84790

Email: edmcarthur@infowest.com

John H. Graham

Professor Emeritus, Department of Biology, Berry College, Mount Berry, GA 30149

Email: jhgraham@berry.edu

Jeffrey J. Duda

Research Ecologist, U.S. Geological Survey, Western Fisheries Research Center, Seattle, WA 98115

Email: jduda@usgs.gov

Jerry Herron

Dean Emeritus, Irvin D. Reid Honors College, Wayne State University, Detroit, MI 48202

Email: jerry.herrin@waynw.edu

Markus Friedrich

Chair and Professor, Department of Biological Sciences, Wayne State University, Detroit, MI 48202

Email: friedrichm@wayne.edu

APPENDIX 1. Publication list of D. Carl Freeman with citations arranged in chronological order.

PUBLICATIONS OF D. CARL FREEMAN

1. FREEMAN, D.C., L.G. KLIKOFF, AND H. EYRING. 1974. Applications of survival theory to ecology. Proceedings of the National Academy of Sciences 71:4332–4335.
2. KLIKOFF, L.G., AND D.C. FREEMAN. 1974. The ecology of cool desert annuals. US/IBP Desert Biome Progress Reports 106. 8 pp.
3. KLIKOFF, L.G., D.C. FREEMAN, AND N. NEGUS. 1975. Ecology of cool desert annuals. US/IBP Desert Biome Progress Reports 87:127–135.
4. FREEMAN, D.C. 1976. Differential resource utilization by the sexes of dioecious plants. Masters's thesis, Brigham Young University, Provo, UT. 26 pp.
5. FREEMAN, D.C., L.G. KLIKOFF, AND K.T. HARPER. 1976. Differential resource utilization by sexes of dioecious plants. Science 193:597–599.
6. FREEMAN, D.C. 1977. Plant dioecy, ecology, evolution, and sex reversal. Doctoral dissertation, Brigham Young University, Provo, UT. 58 pp.
7. HARPER, K.T., D.C. FREEMAN, W.K. OSTLER, AND L.G. KLIKOFF. 1978. A preliminary consideration of the flora of the Great Basin mountain ranges: diversity, sources, and dispersal ecology. Great Basin Naturalist Memoirs 2:81–103.
8. McARTHUR, E.D., A.P. PLUMMER, G.A. VAN EPPS, D.C. FREEMAN, AND K.R. JORGENSEN. 1978. Producing fourwing saltbush in seed orchards. Pages 406–410 *in* D.N. Hyder, editor, Proceedings of the First International Rangeland Congress, Society for Range Management, Denver, CO. 742 pp.
9. FREEMAN, D.C., K.T. HARPER, AND W.K. OSTLER. 1979. Ecology of plant dioecy in the Intermountain Region of western North America and California. Oecologia 44:410–417.
10. BARKER, P.A., D.C. FREEMAN, AND K.T. HARPER. 1980. Sexual flexibility in plants. Proceedings of the International Plant Propagators Society 29:59–66.
11. FREEMAN, D.C., K.T. HARPER, AND E.L. CHARNOV. 1980. Sex change in plants: old and new observations and new hypotheses. Oecologia 47:222–232.
12. FREEMAN, D.C., AND K.T. HARPER. 1980. A relationship between competition and sex ratio of shadscale. Journal of Range Management 33:236–237.
13. FREEMAN, D.C., E.D. McARTHUR, K.T. HARPER, AND A.C. BLAUER. 1981. Influence of environment on the floral sex ratio of monoecious plants. Evolution 35:194–197.
14. McARTHUR, E.D., C.L. POPE, AND D.C. FREEMAN. 1981. Chromosome studies of subgenus *Tridentatae* of *Artemisia*: evidence for autopolyploidy. American Journal of Botany 68:589–605.
15. FREEMAN, D.C., AND E.D. McARTHUR. 1982. Notes: a comparison of twig water stress between males and females of six species of desert shrubs. Forest Science 28:304–308.
16. BARKER, P.A., D.C. FREEMAN, AND K.T. HARPER.1982. Variation in the breeding system of *Acer grandidentatum*. Forest Science 28:563–572.
17. McARTHUR, E.D., AND D.C. FREEMAN. 1982. Sex expression in *Atriplex canescens*: genetics and environment. Botanical Gazette 143:476–482.
18. FREEMAN, D.C., AND E.D. McARTHUR. 1984. The relative influences of mortality, nonflowering, and sex change on the sex ratios of six *Atriplex* species. Botanical Gazette 145:385–394.
19. FREEMAN, D.C., E.D. McARTHUR, AND K.T. HARPER. 1984. The adaptive significance of sexual lability in plants using *Atriplex canescens* as the principal example. Annals of the Missouri Botanical Garden 71:265–277.
20. FREEMAN, D.C., AND J.J. VITALE. 1985. The influence of environment on the sex ratio of spinach. Botanical 21. Gazette 146:137–142.
21. VITALE, J.J., AND D.C. FREEMAN. 1985. Secondary sex characteristics in *Spinacia oleracea* L.: quantitative evidence for the existence of at least three sexual morphs. American Journal of Botany 72:1061–1066.
22. VITALE, J.J., AND D.C. FREEMAN.1986. Partial niche in *Spinacia oleracea*: an examination of reproductive allocation. Evolution 40:426–430.
23. McARTHUR, E.D., S.C. SANDERSON, AND D.C. FREEMAN. 1986. Isozymes of an autopolyploid shrub, *Atriplex canescens* (Chenopodiaceae). Great Basin Naturalist 46:157–160.
24. TIEDEMANN, A.R., E.D. McARTHUR, AND D.C. FREEMAN. 1987. Variations in physiological metabolites and chlorophyll in sexual phenotypes of 'Rincon' fourwing saltbush. Journal of Range Management 40: 151–155.
25. VITALE, J.J., D.C. FREEMAN, L.A. MERLOTTI, AND M. D'ALESANDRO. 1987. Patterns of biomass allocation in *Spinacia oleracea* (Chenopodiaceae) across a salinity gradient: evidence for a niche separation. American Journal of Botany 74:1049–1054.
26. PENDLETON, R.L., E.D. McARTHUR, D.C. FREEMAN, AND A.C. BLAUER. 1988. Heterodichogamy in *Grayia brandegei*: report of a new family. American Journal of Botany 75:267–274.
27. EMLEN, J.M., D.C. FREEMAN, AND F. WAGSTAFF. 1989. Interaction assessment: rationale and test using desert plants. Evolutionary Ecology 3:115–149.
28. FREEMAN, D.C., AND E.D. McARTHUR. 1989. *Atriplex canescens*. Pages 75–86 *in* A.H. Halevy, editor, CRC handbook of flowering. Volume VI. CRC Press, Boca Raton, FL.
29. FREEMAN, D.C., W.A. TURNER, E.D. McARTHUR, AND J.H. GRAHAM. 1991. The characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*). American Journal of Botany 78:805–815.
30. EMLEN, J.M., D.C. FREEMAN, M.B. BAIN, AND J. LI. 1992. Interaction assessment II: a tool for population and community management. Journal of Wildlife Management 56:708–717.
31. McARTHUR, E.D., D.C. FREEMAN, L.S. LUCKINBILL, S.C. SANDERSON, AND G.L. NOLLER. 1992. Are trioecy and sexual lability in *Atriplex canescens* genetically based?: Evidence from clonal studies. Evolution 46:1708–1721.
32. PENDLETON, B.L., D.C. FREEMAN, E.D. McARTHUR, AND R.L. PENDLETON. 1992. Life history features of three sexual morphs of *Atriplex canescens* (Chenopodiaceae) clones grown in a common garden. American Journal of Botany 79:376–382.
33. BICKEL, A., AND D.C. FREEMAN. 1993. Effects of pollen vector and plant geometry on floral sex ratio in monoecious plants. American Midland Naturalist 130:239–247.

34. Emlen, J.M., D.C. Freeman, and J.H. Graham. 1993. Nonlinear growth dynamics and the origin of fluctuating asymmetry. Pages 79–96 *in* T. Markow, editor, Developmental instability: origins and evolutionary significance. Kluwer, Dordrecht, Netherlands.
35. Freeman, D.C., J.H. Graham, and J.M. Emlen. 1993a. Developmental stability in plants: symmetries, stress, and epigenesis. Pages 99–121 *in* T. Markow, editor, Developmental instability: origins and evolutionary significance. Kluwer, Dordrecht, Netherlands.
36. Freeman, D.C., J.H. Graham, and J.M. Emlen. 1993b. Developmental stability in plants: symmetries, stress, and epigenesis. Genetica 89:97–119.
37. Freeman, D.C., E.D. McArthur, S.C. Sanderson, and A.R. Tiedemann. 1993c. The influence of topography on male and female fitness components of *Atriplex canescens*. Oecologia 93:538–547.
38. Freeman, D.C., E.D. McArthur, S.C. Sanderson, and A.R. Tiedemann. 1993d. Influence of topography on cumulative pollen flow of fourwing saltbush. USDA Forest Service Research Note INT-413, Intermountain Research Station, Ogden, UT. 9 pp.
39. Graham, J.H., D.C. Freeman, and J.M. Emlen. 1993a. Developmental stability: a sensitive indicator of populations under stress. Pages 136–158 *in* W.G. Landis, J.S. Hughes, and M.J. Lewis, editors, Environmental toxicology and risk assessment. ASTM International, Philadelphia, PA.
40. Graham, J.H., J.M. Emlen, and D.C. Freeman. 1993b. Developmental stability and its applications in ecotoxicology. Ecotoxicology 2:175–184.
41. Kelly, J.P., D.C. Freeman, and J.M. Emlen. 1993. Competitive impact model for site selection: the impact of competition, affinities and own store cannibalization. International Review of Retail, Distribution and Consumer Research 3:237–257.
42. Byrd, D.W., and D.C. Freeman. 1994. Automated static headspace sampler for gas chromatography. Journal of Chromatography A 686:235–243.
43. Freeman, D.C., and D.W. Byrd. 1994. Statistical treatment of large digital chromatographic data sets. Journal of Chromatography A 686:225–233.
44. Freeman, D.C., J.M. Emlen, J.H. Graham, R.A. Hough, and T.A. Bannon. 1994. Biological monitoring of environmental quality: the use of developmental instability. Journal of Environmental Engineering and Management 4:6–11.
45. Pendleton, B.K., D.C. Freeman, E.D. McArthur, and R.L. Pendleton. 1994. Growth, reproduction, and life history features of *Atriplex canescens* grown in a common garden. Pages 136–139 *in* S.B. Monsen and S.G. Kitchen, compilers, USDA Forest Service General Technical Report INT-GTR-313. Intermountain Research Station, Ogden, UT. 416 pp.
46. Freeman, D.C., B.A. Wachocki, M.J. Stender, D.E. Goldschlag, and H.J. Michaels. 1994. Seed size and sex ratio in spinach: application of the Trivers–Willard hypothesis to plants. Ecoscience 1:54–63.
47. Freeman, D.C., and J.M. Emlen. 1995. Assessment of interspecific interaction in plant communities: an illustration for the cold desert saltbush grassland of North America. Journal of Arid Environments 31: 179–198.
48. Freeman, D.C., J.H. Graham, D.W. Byrd, E.D. McArthur, and W.A. Turner. 1995. Narrow hybrid zone between two subspecies of big sagebrush, *Artemisia tridentata* (Asteraceae). III. Developmental instability. American Journal of Botany 82:1144–1152.
49. Graham, J.H., D.C. Freeman, and E.D. McArthur. 1995. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). II. Selection gradients and hybrid fitness. American Journal of Botany 82:709–716.
50. Tracy, M., D.C. Freeman, J.M. Emlen, J.H. Graham, and R.A. Hough. 1995. Developmental instability as a biomonitor of environmental stress: an illustration using aquatic vegetation. Pages 313–337 *in* F.M. Butterworth, editor, Biomonitors and biomarkers as indicators of environmental change. Plenum Press, NY.
51. Emlen, J.M., D.C. Freeman, J. Escós, and J.M. Alado. 1996. Interaction assessment: predicting the impact of alternative range management actions. Pages 178–181 *in* J.R. Barrow, E.D. McArthur, R.E. Sosebee, and R.J. Tausch, compilers, Proceedings: shrubland ecosystem dynamics in a changing environment. USDA Forest Service General Technical Report GTR-338, Intermountain Research Station, Ogden, UT.
52. Freeman, D.C., J.M. Emlen, J.H. Graham, R.L. Mara, and M. Tracy. 1996. Developmental instability as a bioindicator of ecosystem health. Pages 170–177 *in* J.R. Barrow, E.D. McArthur, R. Sosebee, and R. Tausch, compilers, Proceedings: shrubland ecosystem dynamics in a changing environment. USDA Forest Service General Technical Report GTR-338, Intermountain Research Station, Ogden, UT.
53. Miglia, K.J., and D.C. Freeman. 1996. Delayed pollination, stigma length, sex expression, and progeny sex ration in spinach, *Spinacea oleracea* (Chenopodiaceae). American Journal of Botany 83:326–332.
54. Placzek, J.D., P.J. Roubal, D.C. Freeman, and K. Kulig. 1996. Long term effectiveness of translational manipulation for adhesive capsulitis. Current Orthopaedic Practice 356:181–191.
55. Freeman, D.C., J. Lovett Doust, A. El-Keblawy, K.J. Miglia, and E.D. McArthur. 1997. Sexual specialization and inbreeding avoidance in the evolution of dioecy. Botanical Review 63:65–92.
56. Placzek, J., P. Roubal, D.C. Freeman, and B. Padgett. 1997. Long term effectiveness of gliding manipulation under interscalene brachial plexus block on range of motion, pain and function in adhesive capsulitis patients. Journal Orthopedic Sports Physical Therapy 25:84.
57. Wang, H., E.D. McArthur, S.C. Sanderson, J.H. Graham, and D.C. Freeman. 1997. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). IV. Reciprocal transplant experiments. Evolution 51:95–102.
58. Alados, C.L., J.M. Emlen, B. Wachocki, and D.C. Freeman. 1998a. Instability of development and fractal architecture in dryland plants as an index of grazing pressure. Journal of Arid Environments 38:63–76.
59. Alados, C.L., T. Navarro, B. Cabezun Do, J.M. Emlen, and D.C. Freeman. 1998b. Developmental instability in gynodioecious *Teucrium lusitanicum.* Evolutionary Ecology 12:21–34.
60. Anne, P., F. Mawri, S. Gladstone, and D.C. Freeman. 1998. Is fluctuating asymmetry a reliable biomonitor of stress? A test using life history parameters in soybean. International Journal of Plant Sciences 159:559–565.

61. Emlen, J.M., D.C. Freeman, A. Mills, and J.H. Graham. 1998. How organisms do the right thing: the attractor hypothesis. Chaos 8:717–726.
62. Graham, J.H., J.M. Emlen, D.C. Freeman, L.J. Leamy, and J. Kieser. 1998. Directional asymmetry and the measurement of developmental instability. Biological Journal of the Linnean Society 64:1–16.
63. McArthur, E.D., D.C. Freeman, J.H. Graham, H. Wang, S.C. Sanderson, T.A. Monaco, and B.N. Smith. 1998. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). VI. Respiration and water potential. Canadian Journal of Botany 76:567–574.
64. Placzek, J.D., P.J. Roubal, D.C. Freeman, K. Kulig, S. Nasser, and B.T. Pagett. 1998. Long term effectiveness of translational manipulation for adhesive capsulitis. Clinical Orthopaedics and Related Research 356:181–191.
65. Wang, H., D.W. Byrd, J.L. Howard, E.D. McArthur, J.H. Graham, and D.C. Freeman. 1998. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). V. Soil properties. International Journal of Plant Science 159:139–147.
66. Alados, C.L., J. Escós, J.M. Emlen, and D.C. Freeman. 1999. Characterization of branch complexity by fractal analyses. International Journal of Plant Science 160:S147–S155.
67. Byrd, D.W., E.D. McArthur, H. Wang, J.H. Graham, and D.C. Freeman. 1999. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). VIII. Spatial and temporal pattern of terpenes. Biochemical Systematics and Ecology 27:11–25.
68. El-Keblawy, A., and D.C. Freeman. 1999. Spatial segregation by gender of the subdioecious shrub *Thymelaea hirsuta* in the Egyptian desert. International Journal of Plant Sciences 160:341–350.
69. Freeman, D.C., J.H. Graham, M. Tracy, J.M. Emlen, and C.L. Alados. 1999a. Developmental instability as a means of assessing stress in plants: a case study using electromagnetic fields and soybeans. International Journal of Plant Sciences 160: S157–S166.
70. Freeman, D.C., K. Miglia, E.D. McArthur, J.H. Graham, and H. Wang. 1999b. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): X. Performance in reciprocal transplant gardens. Pages 15–24 *in* E.D. McArthur, W.K. Ostler, and C.L. Wambolt, compilers, Proceedings: shrubland ecotones. USDA Forest Service Proceedings RMRS-P-11, Rocky Mountain Research Station, Ogden, UT.
71. Freeman, D.C., H. Wang, S.C. Sanderson, and E.D. McArthur. 1999c. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). VII. Community and demographic analyses. Evolutionary Ecology Research 1:487–502.
72. Graham, J.H., D.C. Freeman, H. Wang, and E.D. McArthur. 1999. Ecological analysis of the big sagebrush hybrid zone. Pages 11–14 *in* E.D. McArthur, W.K. Ostler, and C.L. Wambolt, compilers, Proceedings: shrubland ecotones. USDA Forest Service Proceedings RMRS-P-11, Rocky Mountain Research Station, Ogden, UT.
73. Smith, B.N., S. Eldredge, D.L. Moulton, T.A. Monoco, A.R. Jones, L.E. Hansen, E.D. McArthur, and D.C. Freeman. 1999. Differences in temperature dependence or respiration distinguish subspecies and hybrid populations of big sagebrush: nature versus nurture. Pages 25–28 *in* E.D. McArthur, W.K. Ostler, and C.L. Wambolt, compilers, Proceedings: shrubland ecotones. USDA Forest Service Proceedings RMRS-P-11, Rocky Mountain Research Station, Ogden, UT.
74. Roubal, P.J., D.C. Freeman, and J.D. Placzek. 1999. Costs and effectiveness of scoliosis screening. Physiotherapy 85:259–268.
75. Wang, H., E.D. McArthur, and D.C. Freeman. 1999. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). IX. Elemental uptake and niche separation. American Journal of Botany 86:1099–1107.
76. Gardocki, M.E., H. Zablocki, A. El-Keblawy, and D.C. Freeman. 2000. Heterocarpy in *Calendula micrantha* (Asteraceae): the effects of competition and water availability on the performance of offspring from different fruit morphs. Evolutionary Ecology Research 2:701–718.
77. McGowen, R.M., D.C. Freeman, and F.M. Butterworth. 2000. A new way to view complex mixtures: measurement of genotoxic effects of mixtures of a polychlorinated bipheynl, a polyaromatic hydrocarbon, and arsenic. *In*: F.M. Butterworth, A. Gunatilaka, and M.E. Gonsebatt, editors, Biomonitors and biomarkers as indicators of environmental change. Volume II. Plenum Publishers, New York, NY. 508 pp.
78. Pendleton, R.L., D.C. Freeman, E.D. McArthur, and S.C. Sanderson. 2000. Gender specialization in heterodichogamous *Grayia brandegei* (Chenopodiaceae): evidence for an alternative pathway to dioecy. American Journal of Botany 87:508–516.
79. Freeman, D.C., J.H. Graham, T. Jones, H. Wang, K.J. Miglia, and E.D. McArthur. 2001. Use of distance measures to assess environmental and genetic variability across sagebrush hybrid zones. Pages 127–133 *in* E.D. McArthur and D.J. Fairbanks, compilers, Shrubland ecosystem genetics and biodiversity: proceedings. USDA Forest Service Proceedings RMRS-P-21, Rocky Mountain Research Station, Ogden, UT.
80. Graham, J.H., E.D. McArthur, and D.C. Freeman. 2001a. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). XII. Galls on sagebrush in a reciprocal transplant garden. Oecologia 126:239–246.
81. Graham, J.H., E.D. McArthur, and D.C. Freeman. 2001b. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). XI. Plant–insect interaction in reciprocal transplant gardens. Pages 118–126 *in* E.D. McArthur and D.J. Fairbanks, compilers, Shrubland ecosystem genetics and biodiversity: proceedings. USDA Forest Service Proceedings RMRS-P-21, Rocky Mountain Research Station, Ogden, UT.
82. Alados, C.L., M.L. Giner, L. Dehasa, J. Escós, F.G. Barroso, J.M. Emlen, and D.C. Freeman. 2002. Developmental instability and fitness in *Periploca laevigata* experiencing grazing disturbance. International Journal of Plant Sciences 163: 969–978.

83. Emlen, J.N., D.C. Freeman, and J.H. Graham. 2002. The adaptive basis of developmental instability: a hypothesis and its implications. Pages 51–61 *in* M. Polack, editor, Developmental instability: causes and consequences. Oxford University Press, New York, NY.
84. Smith, B.N., T.A. Monaco, C. Jones, R.A. Holmes, L.D. Hansen, E.D. McArthur, and D.C. Freeman. 2002. Stress-induced metabolic differences between populations and subspecies of *Artemisia tridentata* (sagebrush) from a single hillside. Thermochimica Acta 394:205–210.
85. Stanton, D.J., E.D. McArthur, D.C. Freeman, and E.M. Golenberg. 2002. No genetic substructuring in *Artemisia* subgenus *Tridentatae* despite strong ecotypic subspecies selection. Biochemical Systematics and Ecology 30:579–593.
86. Freeman, D.C., J.H. Graham, J.M. Emlen, M. Tracy, R.A. Hough, C.L. Alados, and J. Escós. 2003. Plant developmental instability: new measures, applications, and regulation. Pages 367–386 *in* M. Polack, editor, Developmental instability: causes and consequences. Oxford University Press, New York, NY.
87. Graham, J.H., J.M. Emlen, and D.C. Freeman. 2003. Nonlinear dynamics and developmental instability. Pages 35–50 *in* M. Polack, editor, Developmental instability: causes and consequences. Oxford University Press, New York, NY.
88. Tracy, M., D.C. Freeman, J.J. Duda, K.J. Miglia, J.H. Graham, and R.A. Hough. 2003. Developmental instability: an appropriate indicator of plant fitness components? Pages 196–212 *in* M. Polack, editor, Developmental instability: causes and consequences. Oxford University Press, New York, NY.
89. Duda, J.J., D.C. Freeman, J.M. Emlen, J. Belnap, S.G. Kitchen, J.C. Zak, E. Sobek, M. Tracy, and J. Montante. 2003. Differences in native soil ecology associated with invasion of the exotic annual chenopod, *Halogeton glomeratus*. Biology and Fertility of Soils 38:72–77.
90. Emlen, J.M., D.C. Freeman, M.D. Kirchhoff, C.L. Alados, J. Escós, and J.J. Duda. 2003. Fitting population models from field data. Ecological Modeling 162:119–143.
91. Freeman, D.C., M.L. Brown, M. Dobson, Y. Jordan, A. Kizy, C. Micallef, L.C. Hancock, J.H. Graham, and J.M. Emlen. 2003a. Developmental instability: measures of resistance and resilience using pumpkin (*Cucurbita pepo* L.). Biological Journal of the Linnaean Society 78:27–41.
92. Freeman, D.C. J.H. Graham, J.M. Emlen, M.A. Tracy, R.A. Hough, C.L. Alados, and J. Escós. 2003b. Plant developmental instability: new measures, applications, and regulation. Pages 367–386 *in* M. Polak, editor, Developmental instability: causes and consequences. Oxford University Press, New York, NY.
93. Freilich, J.E., J.M. Emlen, J.J. Duda, D.C. Freeman, and P.J. Cafaro. 2003. Ecological effects of ranching: a six-point critique. BioScience 53: 759–765.
94. Graham, J.H., J.M. Emlen, and D.C. Freeman. 2003a. Nonlinear dynamics and developmental instability. Pages 35–50 *in* M. Polak, editor, Developmental instability: causes and consequences. Oxford University Press, New York, NY.
95. Graham, J.H., K. Shimizu, J.M. Emlen, D.C. Freeman, and J. Merkel. 2003b. Growth models and the expected distribution of fluctuating asymmetry. Biological Journal of the Linnaean Society 80: 57–65.
96. Tracy, M., D.C. Freeman, J.J. Duda, K.J. Miglia, J.H. Graham, and R.A. Hough. 2003. Developmental instability: an appropriate indicator of plant fitness? Pages 196–212 *in* M. Polak, editor, Developmental instability: causes and consequences. Oxford University Press, New York, NY.
97. Freeman, D.C., M.L. Brown, J.J. Duda, J.H. Graham, J.M. Emlen, A.J. Krzysik, H. Balbach, D. Kovacic, and J.C. Zak. 2004a. Developmental instability in *Rhus copallinum* L.: multiple stressors, years, and responses. International Journal of Plant Sciences 165:53–63.
98. Freeman, D.C., M.L. Brown, J.J. Duda, J.H. Graham, J.M. Emlen, A.J. Krzysik, H.E. Balbach, D.A. Kovacic, and J.C. Zak. 2004b. Photosynthesis and fluctuating asymmetry as indicators of plant responses to soil disturbance in the Fall Line Sandhills of Georgia: a case study using *Rhus copallinum* and *Ipomoea pandurata*. International Journal of Plant Sciences 165:805–816.
99. Graham, J.H., H.H. Hugie, S. Jones, K. Wrinn, A.J. Krzsik, J.J. Duda, D.C. Freeman, J.M. Emlen, J.C. Zak, D.A. Kovacic, C. Chamberlin-Graham, and H.E. Balbach. 2004. Habitat disturbance and the diversity and abundance of ants (Formicidae) in the southeastern Fall-Line Sandhills. Journal of Insect Science 4:30.
100. Miglia, K.J., D.C. Freeman, E.D. McArthur, and B.N. Smith. 2004. Importance of genotype, soil type, and location on the performance of parental and hybrid big sagebrush reciprocal transplants in the gardens of Salt Creek Canyon. Pages 30–36 *in* A.L. Hild, N.L. Shaw, S.E. Meyer, D.T. Booth, and E.D. McArthur, compilers, Seed and soil dynamics in shrubland ecosystems: proceedings. USDA Forest Service Proceedings RMRS-P-31, Rocky Mountain Research Station, Fort Collins, CO.
101. Placzek, J.D., S.C. Lukens, S. Badalanmenti, P.J. Roubal, D.C. Freeman, K.M. Walleman, A. Parrot, and J.M. Wiater. 2004. Shoulder outcome measures; a comparison of 6 functional tests. American Journal of Sports Medicine 32: 1270–1277.
102. Alados, C.L., Y. Pueyo, D. Navas, B. Cabezudo, A. Gonzalez, and D.C. Freeman. 2005. Fractal analysis of plant spatial patterns: a monitoring tool for vegetation transition shifts. Biodiversity and Conservation 14:1453–1468.
103. Freeman, D.C., M.L. Brown, J.J. Duda, J.H. Graham, J.M. Emlen, A.J. Krzysik, H. Balbach, D.A. Kovacic, and J.C. Zak. 2005. Leaf fluctuating asymmetry, soil disturbance and plant stress: a multiple year comparison using two herbs, *Ipomoea pandurata* and *Cnidoscolus stimulosus*. Ecological Indicators 5:85–95.
104. Krzysik, A.J., H.E. Balbach, D. Kovacic, J. Zak, J.H. Graham, M. Wallace, J. Duda, D.C. Freeman, and J.M. Emlen. 2005. Development of ecological indicator guilds: a site comparison index for the southeast Fall-Line Sandhills. Miscellaneous Publication, SERDP Research Project CS-1114B, SERDP Program Office, Arlington, VA.

105. Miglia, K.J., E.D. McArthur, W.S. Moore, H. Wang, J.H. Graham, and D.C. Freeman. 2005. Nine-year reciprocal transplant experiment in the gardens of the basin and mountain big sagebrush (*Artemisia tridentata*: Asteraceae) hybrid zone of Salt Creek Canyon: the importance of multiple-year tracking of fitness. Biological Journal of the Linnean Society 86:213–225.
106. Golenberg, E.M., and D.C. Freeman. 2006. Environmental sex expression, sexual lability, biased sex ratios and other X-rated stories. Pages 280–291 *in* Floriculture, Ornamental and Plant Biotechnology, Volume IV. Global Science Books, UK.
107. Malone, K.J., T.D. Magnell, D.C. Freeman, M.I. Boyer, and J.D. Placzek. 2006. Surgical correction of dorsally angulated distal radius malunions with fixed angle volar plating: a case series. Journal of Hand Surgery 31:366–372.
108. Cao, A., A.K. Pandya, G.K. Serhatkulu, R.E. Weber, H. Dai, J.S. Thakur, V.M. Naik, R. Naik, G.W. Auner, R. Rabah, and D.C. Freeman. 2007. A robust method for automated background subtraction of tissue fluorescence. Journal of Raman Spectroscopy 38:1199–1205.
109. Freeman, D.C., E.D. McArthur, K.J. Miglia, M.J. Nilson, and M.L. Brown. 2007. Sex and the lonely *Atriplex*. Western North American Naturalist 67: 137–141.
110. Miglia, K.J., E.D. McArthur, R.S. Redman, R.J. Rodriguez, J.C. Zak, and D.C. Freeman. 2007. Genotype, soil type, and locale effects on reciprocal transplant vigor, endophyte growth, and microbial functional diversity of a narrow sagebrush hybrid zone in Salt Creek Canyon, Utah. American Journal of Botany 94:425–436.
111. Graham, J.H., A.J. Krzysik, D.A. Kovacic, J.J. Duda, D.C. Freeman, J.M. Elmen, J.C. Zak, W.R. Long, M.P. Wallace, C. Chamberlin-Graham, J. Nutter, and H. Balbach. 2008. Ant community composition across a gradient of disturbed military landscapes at Fort Benning, Georgia. Southeastern Naturalist 7: 429–448.
112. Graham, J.H., A.J. Krzysik, D.A. Kovacic, J.J. Duda, D.C. Freeman, J.M. Emlen, J.C. Zak, W.R. Long, M.P. Wallace, C. Chamberlin-Graham, J. Nutter, and H. Balbach. 2009. Species richness, equitability, and abundance of ants in disturbed landscapes. Ecological Indicators 9:866–877.
113. Rodriguez, R.J., D.C. Freeman, E.D. McArthur, Y.O. Kim, and R.S. Redman. 2009. Symbiotic regulation plant growth, development, and reproduction. Communicative and Integrative Biology 2:141–143.
114. Sinclair, J., J.M. Emlen, M. Rinella, J. Snelgrove, and D.C. Freeman. 2009. Differential phytosociological interactions involving *Atriplex bonnevillensis*. Western North American Naturalist 69: 475–480.
115. Campbell, W.B., D.C. Freeman, J.M. Emlen, and S. Lopez Ortiz. 2010. Correlations between plant phylogenetic and functional diversity in high altitude cold desert depend on sheep grazing season: Implications for range recovery. Ecological Indicators 10: 676–686.
116. Ferreria, M.M., D.C. Freeman, and R. Zibuk. 2010. Increasing urban middle school students access to authentic math and science experiences through a school community partnership. ERS Spectrum 28: 17–24.
117. Graham, J.H., J.J. Duda, M.L. Brown, S. Kitchen, J.M. Emlen, J. Malol, E. Bankstahl, A.J. Krzysik, H. Balbach, and D.C. Freeman. 2012. The effects of drought and disturbance on the growth and developmental instability of loblolly pine (*Pinus taeda* L.). Ecological Indicators 20:143–150.
118. Sinclair, J.P., J.M. Emlen, and D.C. Freeman. 2012. Biased sex ratios in plants: theory and trends. Botanical Review 78:63–86.
119. Sinclair, J.P., G.D. Maxwell, and D.C. Freeman. 2013a. Consanguineous mating, specialization and the environment: how multiple variable interactions affect the evolution of dioecy. American Journal of Botany 100:1038–1049.
120. Sinclair, J.P., J.L. Korte, and D.C. Freeman. 2013b. The pattern of dioecy in terrestrial, temperate plant succession. Evolutionary Ecology Research 15: 545–556.
121. Sinclair, J.P., D. Kashian, J. Bradford, and D.C. Freeman. 2015. Variation in fractal symmetry of annual growth in aspen as an indicator of developmental stability in trees. Symmetry 7:354–364.
122. Roubal, P.J., M.J. Busito, D.C. Freeman, and J.D. Placzek. 2016. A noninvasive mechanical treatment to reduce the visible appearance of cellulite. Cutis 98:393–398.
123. DeClaire, J.H., P.M. Aiello, O.K. Warritay, and D.C. Freeman. 2017. Effectiveness of bupivacaine liposome injectable suspension for postoperative pain control in total knee arthroplasty: a prospective, randomized, double blind, controlled study. Journal of Arthroplasty 32:S268–S271.
124. Aiello, P.M., D.C. Freeman, O.K. Warritay, and J.H. DeClaire. 2018. Response to letter to the editor on "Effectiveness of bupivacaine liposome injectable suspension for postoperative pain control in total knee arthroplasty: a prospective, randomized, double blind, controlled study." Journal of Arthroplasty 33:302–303.
125. Roubal, P.J., and D.C. Freeman. 2018. Are computer-controlled, pressure modulated knee rehabilitation machines valuable following knee arthroplasty? Global Journal of Orthopedics Research 1:1–8.