Plant exploration for native Hop in the American southwest

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Summary

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Hop (*Humulus lupulus* L.) distribution in the western USA is scattered and uncommon. Two plant collecting expeditions (9–20 September 2002 and 8–19 September 2003) obtained genetic resources of wild American hop (*Humulus lupulus* var. *neomexicanus* Nelson and Cockerell) germplasm from Colorado, Arizona and New Mexico. While herbarium locality data provided a starting point to search for population sites, predictors based on associated species, topography or proximity to water source were inconsistent as locators, particularly in Arizona and New Mexico. In Colorado, populations of this hop variety were more fragmented on the eastern compared with the western slope of the Rocky Mountains. The expeditions sampled 48 populations of *H. l.* var. *neomexicanus* from 18 major drainage basins, resulting in 58 accessions from Colorado, 12 from Arizona and 15 from New Mexico. Herbarium specimens collected from 9 new localities were distributed to major regional herbaria. The living accessions were deposited in the United States Department of Agriculture (USDA), Agricultural Research Service (ARS), National Clonal Germplasm Repository (NCGR), in Corvallis, Oregon, and are available to researchers upon request.

Key words: *Humulus lupulus* var. *neomexicanus*, genetic resources, germplasm

Résumé

Resumen

Introduction

Botanical varieties of North American hop, *Humulus lupulus* L., are poorly represented in world germplasm or breeder collections. Some researchers have suggested that this genus was introduced into America by explorers and settlers from Europe (D. Smith, pers. comm.). However, chemical, morphological and molecular evidence strongly suggests that American hops are taxonomically distinct from the Eurasian *H. lupulus* var. *lupulus* (Small 1978; Hummer et al. 2005). Small (1997, 1978) recognized three varieties of *H. lupulus* endemic to North America based on a numerical analysis of morphological characters (Table 1). The Eurasian *H. l.* var. *lupulus* has become established in North America (Small 1997), especially in the northeast, where potential introgression with native *H. lupulus* varieties is of critical concern to genetic conservation efforts.

The native North American hop gene pool includes the potential for resistance to hop powdery mildew (*Podosphaera macularis* Braun & Takamatsu) (Salmon 1934), viruses (Hampton et al. 2001) and other diseases. Small (1980) researched the pedigree of hop cultivars that had notable resistance to hop powdery mildew, and found that each included a single clonal source of *H. l.* var. *lupuloides* E. Small. In addition, native North American *Humulus* may have insect pest resistance (e.g. aphid), novel growth forms (dwarf, non-vining), low-chill genotypes or unique secondary chemistries. These traits may be valuable to breeding programmes to

Table 1. Summary of key characters distinguishing European and North American *Humulus lupulus* varieties.†

Character	var. *lupulus*	var. *lupuloides*	var. *neomexicanus*	var. *pubescens*
Floral leaf glands	<25/10mm^2	>25/10mm^2	>>25/10mm^2	>25/10mm^2
Floral leaf midrib hairs	<20/cm	<100/cm	>20/cm	>100/cm
Floral leaf surface hairs	absent	usually absent	usually absent	present
Vegetative leaf (>10cm)	<5 lobes	<5 lobes	≥5 lobes	<5 lobes
Distribution	Eurasia; naturalized in eastern North America	central North America	western North America	south central North America

Note: † Observations based on abaxial leaf blade surfaces, after Small (1978, 1997).

broaden the limited genetic base that has been available for the past century.

H. lupulus is a widespread, dioecious, long-lived perennial that is wind pollinated (Small 1997). *Humulus lupulus* has an obligate outcrossing mating system that is typical of other long-lived plants (Ledig 1986). The geographic pattern of genetic variation in widespread outcrossing species requires a sampling strategy that disperses the sample points as much as possible throughout the entire species range (Millar and Libby 1991). Much of the current range of North American *H. lupulus* was either glaciated or cold mixed conifer forest as recent as 10 000 years ago (Delcourt and Delcourt 1993). Only southern areas of the current distribution of *H. lupulus* var. *neomexicanus* Nelson and Cockerell are in regions that were unglaciated with suitable habitat during the Pleistocene (Small 1997; Delcourt and Delcourt 1993). This implies that *H. lupulus* has undergone a rapid expansion of range emanating from southern populations during the Holocene Epoch and is most likely continuing to expand its range (Delcourt and Delcourt 1993; MacDonald and Cwynar 1985). This potential historical impact on genetic variation suggests that: (1) southern populations should have the greatest diversity, both between and within populations, from repeated interglacial introgression and glacial isolation events (Critchfield 1984); (2) genetic diversity within populations will decrease clinally northwards (Millar and Libby 1991); and (3) adaptive and physiological traits may vary clinally from south to north (Cwynar and MacDonald 1987).

In the last two decades, more than 10 American expeditions have collected wild *H. lupulus* material (Hampton et al. 2001; Hummer 2005). North American plant exploration trips began by obtaining representative germplasm from the northern range of *H. lupulus* in Manitoba, Canada, and vicinity, the origin of the first powdery mildew resistant genes recognized and bred into cultivars (Salmon 1934). In 1999 and 2001, Hampton et al. (2001) collected representative germplasm of *H. l.* var. *lupuloides* in North Dakota, as well as Manitoba and Saskatchewan, Canada, and *H. l.* var. *pubescens* E. Small from Missouri in 1999. They also collected in localities from New York to Kentucky in the north-eastern USA (Hummer 2005).

The objective of our collection trips in 2002 and 2003 was to obtain representative genetic resources of hop from the American Southwest. *Humulus lupulus* var. *neomexicanus* is the sole described hop taxon in that region. *Humulus* populations in this area are potentially the most genetically diverse in North America.

Methods

Locality data from *Humulus* herbarium labels were obtained from major regional herbaria, as well as the National Herbarium (US). The Rocky Mountain Herbarium (RM), University of Wyoming, Laramie, WY; University of Colorado Museum Herbarium (COLO), Boulder, CO; Colorado State University Herbarium (CS), Ft. Collins, CO; Adams State College Herbarium (ALAM), Adams State College, Alamosa, CO; University of Arizona Herbarium (ARIZ), Tucson, AZ; Arizona State University Herbarium (ASU), Tempe, AZ; The Deaver Herbarium (ASC), Northern Arizona University, Flagstaff, AZ; University of New Mexico Herbarium (UNM), Albuquerque, NM; and the Biology Herbarium (NMC), New Mexico State University, Las Cruces, NM, provided specimen data for our use. The locality data from these records was mapped to 7.5 minute topographic maps.

The first plant exploration occurred from 9 to 20 September 2002. This trip targeted *H. l.* var. *neomexicanus* from the southern Rocky Mountain region of Colorado and northern New Mexico. The southern Rocky Mountains were divided into 12 major catchments on both sides of the Continental Divide (Table 2). The goal was to sample 3 to 6 populations within each catchment. At each site, we planned to sample from 5 subsites of 1 to 10 individuals, each separated by at least 100 m. However, due to the fragmented distribution pattern, subsites could not always be sampled, so plant material was collected from all possible individuals. The vining growth habit of *Humulus* and its tendency to layer and root at a distance from the original crown made determination of unique clones difficult. The plan to collect at different subsites was to ensure that diverse unique clones would more probably be sampled. Seed were collected whenever possible. Cuttings or rootstocks were collected if seed set was sparse or lacking. When plants were collected, an effort was made to sample both male and female clones.

A second collection trip took place from 8 to 19 September 2003, to Arizona and southern New Mexico. Potential *Humulus* habitat is limited in this region, often on isolated montane islands. The sampling strategy followed the same methods

Table 2. Locality information for collections of *Humulus lupulus* var. *neomexicanus*. (cont.)

State and Location	Latitude	Longitude	Elevation	Catchment	USDA Plant Inventory number	NCGR number
Arizona						
Alpine	33.922	-109.183	2440	Salt	635228	1428
Frye Canyon	32.731	-109.855	1964	Gila	635233	1437
Lookout Canyon	36.582	-112.344	2195	Colorado	635237	1441
Macks Crossing	34.619	-111.093	1953	Little Colorado	635226	1426
McNary	34.046	-109.728	2368	Salt	635227	1427
Mt. Lemmon 1	32.436	-110.759	2305	Santa Cruz	CHUM1430	1430
Mt. Lemmon 2	32.436	-110.759	2305	Santa Cruz	CHUM1431	1431
Oak Creek Canyon	35.023	-111.736	1713	Verde	635225	1424
Pitchfork Canyon	32.644	-109.851	2695	Wilcox Playa	635234	1438
Pitchfork Canyon	32.644	-109.851	2695	Wilcox Playa	635235	1439
Pitchfork Canyon	32.644	-109.851	2695	Wilcox Playa	635236	1440
Walnut Creek	35.115	-111.588	2078	Little Colorado	CHUM1425	1425
Colorado						
Aspen	39.185	-106.808	2437	Colorado	635458	1363
Axial #1	40.263	-107.789	1994	Yampa	635440	1345
Axial #2	40.254	-107.788	2014	Yampa	635441	1346
Axial #3	40.249	-107.785	2025	Yampa	635442	1347
Axial #4	40.270	-107.791	1987	Yampa	635443	1348
Beaver Creek*	40.866	-109.024	1733	Yampa/Green	635444	1349
Buford	39.989	-107.615	2157	White	635447	1352
Cherry Gulch*	37.274	-107.960	2164	San Juan/Animas	635476	1381
Chimney Rock	37.213	-107.298	2025	San Juan/Animas	635472	1377
Coal Creek	39.916	-105.239	1829	South Platte	635429	1333
Cochetopa Creek*	38.458	-106.758	2439	Gunnison	635463	1368
Cordova Plaza	37.134	-104.815	2070	Purgatoire	635486	1392
Deer Gulch #1	39.770	-108.003	2179	White	635450	1355
Deer Gulch #1A	39.770	-108.003	2170	White	635448	1353
Deer Gulch #1B	39.770	-108.003	2170	White	635449	1354
Deer Gulch #2*	39.765	-108.014	2079	White	635451	1356
Delores River	37.590	-108.499	2265	Dolores/San Miguel	635475	1380
Eldorado Canyon S.P.	39.930	-105.297	1890	South Platte	6378p0	1336
Eldorado Springs	39.931	-105.282	1832	South Platte	635432	1337
Hayden East	40.488	-107.159	1975	Yampa	635436	1341
Hayden East 2	40.489	-107.156	1964	Yampa	635438	1343
Hayden West	40.492	-107.299	1939	Yampa	635439	1344
Leopard Creek #1*	38.049	-108.035	2299	Dolores/San Miguel	635473	1378
Leopard Creek #2	38.023	-108.055	2228	Dolores/San Miguel	635474	1379
Mesa Trailhead	39.939	-105.258	1723	South Platte	635430	1334
Miller Creek	39.882	-107.768	2192	White	635445	1350
Milner*	40.487	-107.089	2063	Yampa	635435	1340
Nathrop	38.768	-106.097	2348	Arkansas	635465	1370
Phantom #1	38.569	-105.015	1872	Arkansas	635487	1393
Phantom Canyon #2A	38.550	-105.100	2088	Arkansas	CHUM1400	1400
Phantom Canyon #2A*	38.550	-105.100	2088	Arkansas	CHUM1395	1395

Table 2. Locality information for collections of *Humulus lupulus* var. *neomexicanus*. (cont.)

State and Location	Latitude	Longitude	Elevation	Catchment	USDA Plant Inventory number	NCGR number
Phantom Canyon #2B	38.550	-105.100	2088	Arkansas	CHUM1401	1401
Phantom Canyon #2B	38.550	-105.100	2088	Arkansas	CHUM1396	1396
Phantom Canyon #2C	38.550	-105.100	2088	Arkansas	635488	1397
Phantom Canyon #2D	38.550	-105.100	2088	Arkansas	CHUM1398	1398
Phantom Canyon #2E	38.550	-105.100	2088	Arkansas	CHUM1399	1399
Poncha Creek*	38.455	-106.101	2532	Arkansas	635466	1371
Rattlesnake Gulch	39.931	-105.291	1890	South Platte	635431	1335
Redstone Creek #1	40.515	-105.188	1722	South Platte	635433	1338
Redstone Creek #2	40.567	-105.230	1813	South Platte	635434	1339
Rifle East #1	39.648	-107.708	1887	Colorado	635452	1357
Rifle East #2	39.691	-107.703	2009	Colorado	635453	1358
Rock Creek #1	37.495	-106.236	2514	Rio Grande	635469	1374
Rock Creek #2	37.490	-106.260	2530	Rio Grande	635470	1375
Sangre de Cristo #1	37.495	-105.334	2409	Rio Grande	635467	1372
Sangre de Cristo #2	37.531	-105.295	2541	Rio Grande	635468	1373
Silver Plume	39.697	-105.724	2791	South Platte	635457	1362
South Fork Campground	39.868	-107.535	2338	White	635446	1351
Sweetwater #1	39.810	-107.182	2366	Colorado	635454	1359
Sweetwater #2	39.810	-107.171	2363	Colorado	635455	1360
Sweetwater #3	39.798	-107.161	2363	Colorado	635456	1361
Tomichi Creek	38.414	-106.512	2518	Gunnison	635464	1369
Wagon Wheel	37.769	-106.800	2537	Rio Grande	635471	1376
West Plum Creek	39.429	-104.969	1779	South Platte	635491	1402
Willow Creek	38.453	-107.058	2357	Gunnison	635459	1364
Willow Creek A*	38.453	-107.058	2374	Gunnison	635460	1365
Willow Creek B	38.453	-107.059	2374	Gunnison	635461	1366
Willow Creek C	38.453	-107.059	2374	Gunnison	635462	1367
Wolf Creek	40.509	-107.131	2032	Yampa	635437	1342
Wootten	37.019	-104.491	2201	Purgatoire	635485	1391
New Mexico						
Bear Trap Canyon	33.810	-107.587	2302	Rio Grande	635232	1434
Bear Trap Canyon	33.810	-107.587	2302	Rio Grande	CHUM1436	1435
Bear Trap Canyon	33.810	-107.587	2302	Rio Grande	CHUM1437	1436
Carlton Canyon	33.396	-105.757	2644	Pecos	635230	1432
Cimarron River #1	36.538	-105.227	2533	Canadian	635483	1389
Cimarron River #2	36.537	-105.206	2455	Canadian	635484	1390
Gilita Creek	33.409	-108.574	2403	Gila	635229	1429
Las Huertas Creek	35.250	-106.411	2149	Rio Grande	635477	1382
Manuelitas Creek	35.809	-105.288	2176	Canadian	635482	1388
Pecos #1	35.717	-105.680	2328	Pecos	637831	1383
Pecos #1F	35.717	-105.680	2328	Pecos	635478	1384
Pecos #1M	35.717	-105.680	2328	Pecos	635479	1385
Pecos #2	35.737	-105.678	2354	Pecos	635481	1387
Pecos #2F	35.737	-105.678	2354	Pecos	635480	1386
Windy Point	33.406	-105.757	2796	Pecos	635231	1433

Table 3. Habitat and sample information for collections of *Humulus lupulus* var. *neomexicanus* L. (cont.)

State and Location	Habitat	Form†/sex	Amount	Cone length‡ mean ±SD (mm)	USDA Plant Inventory number	NCGR number
Arizona				±		
Alpine	willow thickets	SD	2 000	46 ±4.0	635228	1428
Frye Canyon	riparian closed canopy	PL/F	1	27 ±1.5	635233	1437
Lookout Canyon	dry rocks	PL/F	1	20 ±3.5	635237	1441
Macks Crossing	riparian open canopy	SD	2000	32 ±4.4	635226	1426
McNary	willow thickets	SD	1 250	38 ±4.6	635227	1427
Mt. Lemmon 1	willow thickets	PL/F	1	35 ±1.5	CHUM1430	1430
Mt. Lemmon 2	willow thickets	PL/F	1	30 ±1.5	CHUM1431	1431
Oak Creek Canyon	riparian closed canopy	SD	500	48 ±7.5	635225	1424
Pitchfork Canyon	dry rocks	PL/F	1	30 ±3.0	635234	1438
Pitchfork Canyon	dry rocks	PL/M	1		635235	1439
Pitchfork Canyon	dry rocks	SD	250		635236	1440
Walnut Creek	riparian open canopy	PL/F	1	37 ±5.9	CHUM1425	1425
Colorado						
Aspen	dry rocks	SD	5 760		635458	1363
Axial #1	riparian open canopy	SD	14 800		635440	1345
Axial #2	riparian open canopy	SD	21 670		635441	1346
Axial #3	riparian open canopy	SD	3 900		635442	1347
Axial #4	riparian open canopy	SD	7 200		635443	1348
Beaver Creek	willow thickets	SD	5 220	26 ±1.7	635444	1349
Buford	riparian closed canopy	SD	56 145		635447	1352
Cherry Gulch	willow thickets	SD	9 080	31 ±3.5	635476	1381
Chimney Rock	riparian open canopy	SD	6 895		635472	1377
Coal Creek	riparian open canopy	SD	1 830		635429	1333
Cochetopa Creek	riparian open canopy	SD	46 000	39 ±15.3	635463	1368
Cordova Plaza	willow thickets	SD	17 590		635486	1392
Deer Gulch #1	riparian open canopy	PL/M	2		635450	1355
Deer Gulch #1A	riparian open canopy	PL/F	2		635448	1353
Deer Gulch #1B	riparian open canopy	PL/F	2		635449	1354
Deer Gulch #2	riparian open canopy	SD	51	26 ±0.6	635451	1356
Delores River	riparian closed canopy	SD	80		635475	1380
Eldorado Canyon S.P.	riparian open canopy	SD	1 600		637830	1336
Eldorado Springs	dry rocks	SD	10 360		635432	1337
Hayden East	riparian closed canopy	SD	7 740		635436	1341
Hayden East 2	riparian closed canopy	SD	5 850		635438	1343
Hayden West	riparian closed canopy	SD	22 640		635439	1344
Leopard Creek #1	riparian closed canopy	SD	6 700	32 ±3.6	635473	1378
Leopard Creek #2	riparian closed canopy	SD	7 900		635474	1379
Mesa Trailhead	willow thickets	SD	3 500		635430	1334
Miller Creek	willow thickets	SD	35 090		635445	1350
Milner	riparian closed canopy	SD	25 980	38 ±4.9	635435	1340
Nathrop	willow thickets	SD	22 380		635465	1370
Phantom #1	riparian closed canopy	SD	3 235		635487	1393
Phantom Canyon #2A	dry rocks	PL/M			CHUM1400	1400
Phantom Canyon #2A	dry rocks	PL/F	1	21 ±1.5	CHUM1395	1395
Phantom Canyon #2B	dry rocks	PL/M			CHUM1401	1401

Table 3. Habitat and sample information for collections of *Humulus lupulus* var. *neomexicanus* L. (cont.)

State and Location	Habitat	Form†/sex	Amount	Cone length‡ mean ±SD (mm)	USDA Plant Inventory number	NCGR number
Phantom Canyon #2B	dry rocks	PL/F	1		CHUM1396	1396
Phantom Canyon #2C	dry rocks	PL/F	1		635488	1397
Phantom Canyon #2D	dry rocks	PL/F	1		CHUM1398	1398
Phantom Canyon #2E	dry rocks	PL/F	1		CHUM1399	1399
Poncha Creek	riparian open canopy	SD	21 500	21 ±2.5	635466	1371
Rattlesnake Gulch	dry rocks	SD	4 700		635431	1335
Redstone Creek #1	riparian open canopy	SD	7 785		635433	1338
Redstone Creek #2	riparian open canopy	SD	5 320		635434	1339
Rifle East #1	riparian open canopy	SD	19 000		635452	1357
Rifle East #2	riparian closed canopy	SD	20 965		635453	1358
Rock Creek #1	riparian open canopy	SD	3 765		635469	1374
Rock Creek #2	riparian open canopy	SD	3 100		635470	1375
Sangre de Cristo #1	willow thickets	SD	2 565		635467	1372
Sangre de Cristo #2	willow thickets	SD	6 940		635468	1373
Silver Plume	riparian closed canopy (urban)	SD	17 940		635457	1362
South Fork Campground	willow thickets	SD	35 000		635446	1351
Sweetwater #1	dry rocks	SD	9 640		635454	1359
Sweetwater #2	willow thickets	SD	28 180		635455	1360
Sweetwater #3	willow thickets	SD	4 900		635456	1361
Tomichi Creek	riparian closed canopy	SD	2 000		635464	1369
Wagon Wheel	dry rocks	SD	16 075		635471	1376
West Plum Creek	willow thickets	SD	12 910		635491	1402
Willow Creek	dry rocks	SD	890		635459	1364
Willow Creek A	riparian closed canopy	PL/F	3	19 ±1.0	635460	1365
Willow Creek B	riparian closed canopy	PL/F	1		635461	1366
Willow Creek C	riparian closed canopy	PL/M	1		635462	1367
Wolf Creek	riparian closed canopy	SD	715		635437	1342
Wootten	riparian closed canopy	SD	7 000		635485	1391
New Mexico						
Bear Trap Canyon	dry rocks	PL/F	1		635232	1434
Bear Trap Canyon	dry rocks	PL/M	1		CHUM1436	1435
Bear Trap Canyon	dry rocks	PL/?	1		CHUM1437	1436
Carlton Canyon	dry rocks	PL/F	1	39 ±6.5	635230	1432
Cimarron River #1	riparian closed canopy	SD	100		635483	1389
Cimarron River #2	willow thickets	SD	13 565		635484	1390
Gilita Creek	willow thickets	SD	1 200	37 ±13.3	635229	1429
Las Huertas Creek	riparian closed canopy	SD	7 880		635477	1382
Manuelitas Creek	willow thickets	SD	21 650		635482	1388
Pecos #1	dry rocks	SD	16		637831	1383
Pecos #1F	dry rocks	PL/F	6		635478	1384
Pecos #1M	dry rocks	PL/M	1		635479	1385
Pecos #2	dry rocks	SD	365		635481	1387
Pecos #2F	dry rocks	PL/F	5		635480	1386
Windy Point	dry rocks	PL/F	1		635231	1433

Notes: † forms: SD = seed; PL = plant. ‡ Mean of three cone samples for each location; SD = Standard Deviation.

as the first trip. In addition, we used the Ecological Niche Modelling tool of DIVA-GIS Version 3 (www.diva-gis.org) to predict distribution based on annual mean precipitation, annual mean temperature and temperature extremes of the 2002 collection localities. The collecting localities of both trips were grouped into four basic habitat types: riparian closed canopy, riparian open canopy, willow thickets and dry rocks (Table 3). These types are listed in order of decreasing soil moisture availability to the hop plants.

Cone length for samples was measured from digital images (Arizona and New Mexico samples) or herbarium vouchers (Colorado samples) (Table 3). For each sample, 3 cones were measured.

Results and discussion

Humulus lupulus var. *neomexicanus* was observed and collected from 48 populations throughout the 18 major drainage basins in the southern Rocky Mountains (Colorado and northern New Mexico) and montane Southwest United States (Arizona and southern New Mexico) (Tables 2 and 3, Figure 1). These collections resulted in 60 seed and 28 plant accessions. Abundant seed was collected from populations in Colorado and northern New Mexico, but in southern New Mexico and Arizona, seed was rare or absent. In 6 of these locations, only a single, unpollinated female plant was found (Table 3).

The seed and plant accessions were deposited at the USDA ARS NCGR in Corvallis, Oregon. Specimens were collected from 9 populations in Colorado, representing previously unrepresented localities for the herbaria (Table 2). These specimens have been distributed to the following herbaria: CS, CO, NM, RM and US.

Cone size was variable among populations. Cone lengths for 21 populations are presented (Table 3), with mean (n = 3) cone length, ranging from 19 mm at Willow Creek, Colorado, to 48 mm at Oak Creek Canyon, Arizona. Small (1997) considered cone lengths of 20 to 30 mm typical, varying from 10 to 60 mm. Cone length did not appear to be associated with habitat type (Table 3). This may indicate that the variability of cone length has a larger genetic than environmental component.

Small (1978) defined *H. l.* var. *neomexicanus* as having leaves with relatively more lobes, deeper lobe clefts and greater density of abaxial leaf glands than observed in other *H. l.* varieties (Table 1). The plants collected on both trips matched this description. Leaf morphology, however, was variable. Mature leaves varied from five-lobed to laciniate. The abaxial leaf glands were dense but not visibly variable. Cone aroma was variable among populations (data not shown). Powdery mildew was observed on plants only at Silver Plume, Colorado. Silver Plume was the only urban collecting site that was visited (Table 3) and European hop cultivars (*H. l.* var. *lupulus*) may have been introduced to that city and mildew could have been introduced as well. The Silver Plume plants that were collected, however, were the wild American hop, *H. l.* var. *neomexicanus*. In preliminary greenhouse studies,

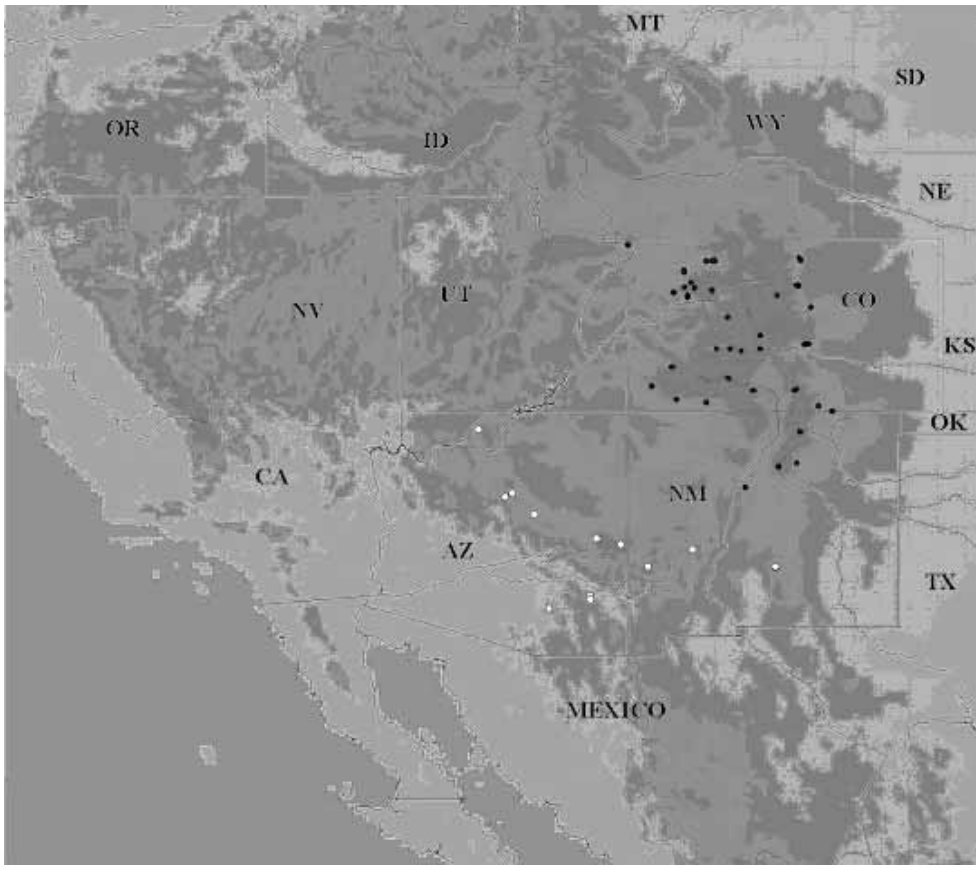

Figure 1. Hop (*Humulus lupulus* var. *neomexicanus*) collection sites in 2002 (black dots) and 2003 (white dots).

H. l. var. *neomexicanus* plants were moderately to highly susceptible to powdery mildew (data not shown).

These observations concur with that of Small (1997), that *Humulus* distribution in the western USA is scattered and uncommon. *Humulus* appears to have an opportunistic, fragmented distribution pattern and may be undergoing range expansion or local extinction. While herbarium locality data provided a starting point to search for population sites, predictors based on associated species, topography or proximity to a water source were inconsistent as locators, particularly in Arizona and New Mexico. The Diva-GIS program predicted well the general habitat of *Humulus*, including major riparian zones, but this predicted habitat was of little practical value because specific *Humulus* sites are so highly localized (data not shown). This lack of correlation of actual *Humulus* localities with predicted habitat suggests *Humulus* distribution is not in equilibrium with its potential distribution and that other factors are involved, such as limited seed and pollen dispersal. The most stable habitat for *Humulus* was near perennial streams with a well-developed cover of willow (*Salix* spp.). Another, alternative, situation was at the base of rocks in a riparian corridor where the stream is at a distance or seasonal. In the Rocky Mountains, *Humulus* was much more fragmented on the eastern than on the western slope. Human encroachment has increased on the eastern slope of the Rocky Mountains (West 1988). This, and the drier climate (West 1988), may have contributed to the loss of habitat and reduction in the numbers of hop plants that were observed, in contrast to the referenced herbarium localities.

In Arizona and southern New Mexico, the focus was on southern isolated *Humulus* localities, and 21 localities were visited based on herbarium label data showing where *Humulus* had previously been collected. *Humulus* was found at 11 of these localities. Two additional populations were discovered *en route*. In the 10 localities where *Humulus* was not found, local extinction was possibly caused by degraded habitat or vegetation change. Hampton et al. (2001) reported a similar loss of populations of *H. l.* var. *lupuloides* and attributed the loss to grazing or human encroachment on native habitat. The increase in juniper (*Juniperus scopulorum* Sarg.) cover throughout the south-western USA has been suggested as a probable cause for reduction in surface stream flow during the last 150 years (West 1988). The combination of overgrazing and juniper growth may be causing local extinction of *H. l.* var. *neomexicanus*, especially in marginal habitats.

Conclusions and further exploration

Some of the natural range of *H. l.* var. *neomexicanus* in the USA has been successfully sampled. Further collecting from northern Arizona, north-west New Mexico, Nevada, Utah, and northern Mexico would complete the survey of this botanical variety. Existing populations in marginal habitats along the southern distributional range of *H. lupulus* may become extinct, just as many of the populations from which previous collections were made 50 to 100 years ago are no longer extant. Global climate change models predict that both precipitation and evaporation in the American Southwest will increase, resulting in drier summers and dramatic changes in potential vegetation (VEMAP Members 1995). The overall distribution of *Humulus* may expand northward into Canada and possibly westward into the Great Basin. The effect in terms of local population change is uncertain and is more likely to depend on the availability of suitable quality riparian habitat than on regional climate change.

Introgression and loss of habitat are considered to be significant threats to *in situ* conservation efforts in widespread species complexes (Millar and Libby 1991). Fortunately, most of the habitat of *H. l.* var. *neomexicanus* we observed occurs on publicly owned lands managed by federal agencies. This affords reasonable protection from development and provides baseline security for *in situ* conservation. The genetic diversity within *H. l.* var. *pubescens* and *H. l.* var. *lupuloides*, however, is threatened not only through loss of habitat from human development, but, more importantly, by introgression from naturalized *H. l.* var. *lupulus*. Since *H. l.* var. *neomexicanus* and *H. l.* var. *pubescens* are still poorly represented in *ex situ* collections (Hummer 2005), further exploration is recommended. These and other recent collecting trips provide the opportunity for further botanical, morphological, chemical and molecular investigation into native *Humulus*.

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