Susceptibility of Hop Cultivars to Downy Mildew: Associations with Chemical Characteristics and Region of Origin

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ABSTRACT

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Hop downy mildew (caused by *Pseudoperonospora humuli*) is a yield-limiting disease in many hop-production regions of the world. In this research, 110 cultivars that are or were widely grown in the United States, Europe, or Australasia were evaluated in western Oregon over three years for their reaction to the shoot infection phase of downy mildew and vigor. There was a large range of downy mildew susceptibility and vigor amongst commercial cultivars, with some cultivars possessing a very high level of resistance. Overall, however, disease resistance and vigor were significantly greater in cultivars originating from Europe than those originating from the United States, Japan, and Australia/New Zealand. Amongst a subset of 79 cultivars, vigor was negatively correlated with levels, in cones, of cohumulone, a chemical constitute of bittering acids typically found in germplasm derived from North America. The generally poor vigor observed in cultivars derived outside of Europe likely is indicative of a lack of tolerance to the crown infection phase of the disease. Thus, the best sources of downy mildew resistance seems to be found in cultivars from the United Kingdom and continental Europe, and such cultivars are typically lower yielding and lack distinctive aroma and flavor characteristics presently desired by craft brewers. Introgression of downy mildew resistance into North American germplasm with high yield and desirable brewing characteristics is needed.

INTRODUCTION

Hop downy mildew, caused by *Pseudoperonospora humuli* (Miy. et Tak.) Wils., is a major disease of hop (*Humulus lupulus*) in most growing regions of the world (Neve 1991; Johnson et al. 2009). First identified in Japan in 1905, downy mildew became a worldwide problem by the 1930s (Royle and Kremheller 1981; Johnson et al. 2009). The use of strict quarantine regulations has kept Australia, New Zealand, and South Africa free of the disease (Neve 1991).

Hop shoots systemically infected with the hop downy mildew pathogen have stunted growth, shortened internodes, and downward-curled leaves. These infected shoots are often referred to as "spikes" owing to their resemblance to wheat spikes. Shoot infection is thought to arise from infected crown buds (resulting in so-called "primary spikes") or from later infection of apical meristems ("secondary spikes") (Royle and Kremheller 1981; Johnson et al. 2009). Infected shoots generally will not climb and must be physically removed and replaced with healthy shoots. The disease can cause complete crop damage in several ways, namely loss of cone-bearing lateral branches and cones, reduction in yield due to infection of trained bines, and a decrease in vigor or plant death due to infection of the root system (Royle and Kremheller 1981; Johnson and Anliker 1985; Johnson et al. 2009; Neve 1991). The pathogen overwinters as mycelium in the hop crown, infecting crown buds, which form primary basal spikes in the spring that initiate the disease cycle (Coley-Smith 1962; Johnson and Anliker 1985; Royle and Kremheller 1981). In some regions, oospores are formed abundantly in diseased tissue, although the role of oosporic inoculum in disease development remains uncertain (Johnson et al. 2009; Royle and Kremheller 1981). Disease outbreaks can be polyetic, as individual plants can become chronically infected and consistently produce basal spikes. This leads to greater numbers and earlier emergence of diseased shoots in subsequent seasons (Salmon and Ware 1925; Johnson and Anliker 1985; Neve 1991; Gent et al. 2010).

Commercial production of hops relies on sanitation, crown pruning, and fungicides as the main management tools for downy mildew (Skotland and Johnson 1983; Neve 1991; Gent and Ocamb 2009; Gent et al. 2010; Gent et al. 2012). While the most efficacious management tool is the production of resistant cultivars, no cultivars are completely immune to downy mildew and resistance appears to be highly quantitative and polygenic (Royle and Kremheller 1981; Neve 1991; Johnson et al. 2009; Henning et al. 2015). Some cultivars are highly susceptible to the crown rot phase of the disease (e.g., Cluster), while others can withstand some crown infection but are highly susceptible to the foliar phase of the disease (e.g., Nugget) (Coley-Smith 1964; Neve 1991; Johnson et al. 2009). In cultivars that are susceptible to the crown rot phase, mycelium invades crown buds and infected buds are often killed, leading to low vigor and eventual plant death (Coley-Smith 1964; Neve 1991). Carbohydrate levels in the root system also are depleted more rapidly in infected plants, contributing to a progressive decline in vigor and yield over time (Williams et al. 1961).

Variation in susceptibility to the crown rot phase of the disease can affect the interpretation of downy mildew disease assessments conducted in a field setting (Neve 1991). In cultivars resistant to

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the crown rot phase of downy mildew, there is a positive correlation between basal spikes produced in one season and the number of basal spikes produced the following spring (Johnson and Anliker 1985). Neve (1991) stated that there is an inverse relationship between crown rot susceptibility and the incidence of primary basal spikes. He noted that Bullion (susceptible to crown rot) produced few spikes, but numerous plants died, while Northern Brewer (resistant to crown rot) produced numerous spikes without plant death. Consequently, assessment of resistance to shoot infection due to downy mildew requires assessment of both the frequency of shoot infection and total shoot production over time.

In the Pacific Northwest, not all phases of the disease are equally important due to the generally warm, dry summers that limit late-season disease development (Neve 1991; Johnson et al. 2009; Gent and Ocamb 2010). For example, in the mid-twentieth century, Bullion, bred in the United Kingdom by Salmon (1938), was grown extensively in western Oregon and the Yakima Valley of Washington because the plants did not succumb to crown rot by downy mildew when grown in these environments. In contrast, when grown in the United Kingdom, Bullion was highly susceptible to crown infection (Neve 1991). In western Oregon, downy mildew tends to be most prevalent during vegetative development of shoots in spring and late-season attack of the disease is less frequent than in the United Kingdom (Gent and Ocamb 2009; Gent et al. 2010).

Regional effects are known to exist for certain agronomic and chemical traits of cultivars that are developed and adapted to growing in particular areas (Neve 1991). Henning et al. (2004a) used phenotypic data of 129 world hop cultivars grown in Oregon and identified five diversity groups (clusters) of hop cultivars with similar characteristics that were largely explained by geographic origins. While disease assessments were not conducted in the study by Henning et al. (2004a), it is possible that there is an association between region of origin and downy mildew resistance (Neve 1991). Collecting disease assessments in one location greatly increases the accuracy and value of the data because cultivars can behave differently in different environments. While downy mildew resistance has been quantified for a number of world hop cultivars, this data often has been collected and collated from multiple locations using different evaluation methods. Consistent documentation and quantitative evaluations have not been compiled for a diverse collection of cultivars for the Pacific Northwestern United States. The data presented in this paper addresses this need, and provides a uniform assessment of downy mildew disease reaction in western Oregon for a large collection of hop cultivars. Further, we sought to correlate cone chemical properties, yield, and region of origin of cultivars with downy mildew phenotype.

DOWNY MILDEW ASSESSMENTS

Assessments of downy mildew phenotype were conducted in experimental plots near Corvallis, OR. The plot contained 110 cultivars that are or were widely grown in the United States, Europe, or Australasia as described by Henning et al. (2004a). Each cultivar was planted in single plant plots, from rhizomes or young potted plants, with four replicate plants. These cultivars were collected over a period of 25 years, and all cultivars evaluated had been established since at least 1999. Plots were maintained using standard production practices for hop as noted by Henning et al. (2004a). However, no fungicide applications were made for at least four years before disease assessments began. In hop production, spring pruning is a common horticultural practice used to set training dates of shoots, and the timing and thoroughness of pruning can influence the severity of downy mildew (Gent et al. 2012). Plants were not pruned in 2005, but shoots were chemically pruned (desiccated) using carfentrazone herbicide (33.6 g/ha as Aim EC, FMC, Philadelphia, PA) during late March in 2006 and early April in 2007.

Assessments of downy mildew were conducted during each growing season from 2005 to 2007. Every 14 days, each plant was inspected for the presence of basal spikes. The total number of shoots (both healthy and affected by downy mildew) also was enumerated as a correlate of plant vigor. Evaluations began in mid-April each year and three to four evaluations were conducted each year. Enumerating total shoots per plant and total basal spikes produced allowed disease susceptibility to be expressed as a proportion of total shoots, giving an indication of disease severity. The proportion of shoots with downy mildew provides a quantitative measurement of susceptibility to the shoot infection phase of the disease, but as described previously, the number of infected shoots produced is also influenced by the resistance or tolerance of a plant to the crown infection phase of the disease. When the proportion of shoots that are infected is considered jointly with the total number of shoots produced, it is possible to identify cultivars with both resistance to shoot infection and, putatively, tolerance to crown infection as described below.

For each cultivar, disease incidence was averaged over sampling dates within a year because disease assessments were always evenly spaced in time. The proportion of shoots with downy mildew and total shoots produced was initially summarized as the mean over each year. The proportion of shoots with downy mildew and total shoots varied among cultivars (Table 1), with mean proportion of shoots with downy mildew ranging from near 0 to 0.50 and mean total shoots ranging from 3.4 to 67.6. Cultivars Blue Northern Brewer, Cluster L16, and Pacific Gem were planted in the yard but all plants were dead in two or three years of the evaluations, and therefore excluded from the analyses. These cultivars are reported to be highly susceptible to downy mildew (Johnson et al. 2009; Mitchell et al. 2011), and downy mildew likely is the reason these cultivars died, although other causes of death cannot be ruled out.

The data from the individual cultivars was plotted based on the mean incidence of shoots with downy mildew and shoots produced per plant. The relationship of downy mildew susceptibility and total shoot production varied among hop cultivars (Figure 1; see Table 1 for reference numbers). The upper left-hand quadrant illustrates cultivars that had vigor greater than the mean of the entire data set and the proportion of shoots with downy mildew less than the mean of the entire data set. Cultivars in this quadrant are expected to possess the greatest level of resistance to the foliar phase of the disease and also the greatest level of tolerance to crown infection. The upper right-hand quadrant illustrates cultivars that were vigorous but susceptible to shoot infection. The lower left-hand quadrant depicts cultivars that had a small proportion of shoots infected with downy mildew, but were not vigorous. Cultivars in this quadrant appear to have either inherent low vigor or do not tolerate crown infection, as typified by Cluster L16. The lower right-hand quadrant illustrates cultivars that were not vigorous and also highly susceptible to downy mildew.

It is impossible in this study to disentangle cultivars with low vigor due to lack of adaptation to the environment from those with poor vigor resulting from susceptibility to the crown infection phase of downy mildew. However, for breeding purposes, this distinction may not be critical because cultivars

TABLE 1
Proportion of shoots with downy mildew (DM), mean shoots per plant, and the corresponding origin designation for world hop cultivars grown in Corvallis, OR during 2005 to 2007.

Ref. No.	Accession No.[x]	Cultivar	Proportion of shoots with DM	Shoots per plant	Origin[z]
1	21050	Ahil	0.15	29.3	EU
2	66050	Alliance	0.22	37.7	UK
3	21406	AlphAroma	0.20	65.7	–
4	21051	Apolon	0.04	55.2	EU
5	21222	Aquila	0.19	9.6	USA
6	21052	Atlas	0.19	27.2	EU
7	21053	Aurora	0.18	55.5	EU
8	21080	Backa	0.22	15.7	EU
9	21287	Banner	0.29	34.8	USA
10	21698	Bianca	0.27	36.1	USA
11	21238	Blisk	0.04	56.2	-
12	21079	Blue Northern Brewer[y]	0	0	EU
13	21239	Bobek	0.24	43.4	EU
14	19001	Brewer's Gold	0.15	18.7	USA
15	21056	Bullion 10A v.f.	0.29	33.8	–
16	21709	C-601	0.18	23.9	–
17	66054	Calicross	0.33	39.8	AUS
18	21679	Canadian Red Vine	0.31	35.9	–
19	21681	Canterbury Golding	0.21	19.7	UK
20	56013	Cascade	0.26	46.8	USA
21	21613	Cekin	0.02	37.7	–
22	21611	Celeia	0.05	55.9	EU
23	21507	Centennial	0.29	15.6	–
24	21612	Cerera	0.02	67.6	–
25	21226	Chinook	0.19	28.3	USA
26	21614	Cicero	0.002	50.2	–
27	21011	Cluster L16[y]	0	3.4	–
28	21040	Columbia	0.09	14.1	USA
29	62013	Comet	0.23	9.2	USA
30	21490	Crystal	0.28	38.3	USA
31	62052	Density	0.27	44.6	-
32	21081	Dunav	0.01	56.7	EU
33	21276	Early Prolific	0.34	34.8	UK
34	21277	Early Promise	0.14	21.4	UK
35	21678	Eastern Gold	0.14	13.2	JAPAN
36	21669	Eastwell Golding	0.20	30.9	–
37	21170	Elsasser	0.37	25.0	EU
38	21183	Eroica	0.29	33.1	USA
39	66055	First Choice	0.31	26.5	AUS
40	48209	Fuggle H	0.06	50.5	UK
41	21016	Fuggle N v.f.	0.09	56.5	–
42	21701	Furano Ace	0.28	55.1	–
43	21182	Galena	0.27	25.2	USA
44	21039	Golden Star	0.14	17.9	JAPAN
45	21404	Green Bullet	0.16	2.2	–
46	21671	Hallertauer Gold	0.003	42.4	EU
47	21014	Hallertauer Mittelfrüher	0.39	37.0	EU
48	21670	Hallertauer Magnum	0.01	60.3	EU
49	21672	Hallertauer Tradition	0.001	46.4	EU
50	21673	Hersbrucker Pure	0.20	45.9	EU
51	21373	Horizon	0.37	15.3	–
52	21097	Hueller Bitterer	0.02	34.1	EU
53	21167	Hybrid-2 (India)	0.23	40.0	–
54	21680	Kent Golding	0.23	26.4	UK
55	21278	Keyworth's Early	0.25	13.0	UK
56	21279	Keyworth's Midseason	0.33	52.3	–
57	21700	Kirin C-827	0.05	29.0	–
58	21286	Kirin II	0.23	36.3	JAPAN
59	21677	Kitamidori	0.19	31.8	JAPAN

(continued)

TABLE 1 (continued)

Ref. No.	Accession No.[x]	Cultivar	Proportion of shoots with DM	Shoots per plant	Origin[z]
60	21172	Landhopfen	0.29	18.8	EU
61	21457	Liberty	0.03	27.1	–
62	21523	Lublin v.f.	0.17	28.3	–
63	21455	Mt. Hood	0.28	31.8	USA
64	21093	Nadwislanska	0.24	21.2	EU
65	21114	Neoplanta	0.02	44.7	EU
66	21082	Northern Brewer	0.28	30.3	UK
67	21193	Nugget	0.35	44.6	USA
68	21610	New Zealand Hallertauer	0.11	18.9	–
69	21225	Olympic (herm)	0.33	48.3	USA
70	21667	Omega	0.03	33.5	UK
71	21675	Orion	0.001	53.9	EU
72	21609	Pacific Gem (NZ)[y]	0	0	AUS
73	21227	Perle	0.001	36.9	EU
74	68052	Petham Golding	0.50	54.7	–
75	21168	Precoce d'Bourgogne	0.26	10.6	EU
76	21280	Pride of Kent	0.33	40.3	UK
77	66052	Pride of Ringwood	0.13	3.1	AUS
78	21077	Saazer	0.31	28.3	EU
79	21664	Santiam	0.31	40.2	–
80	61020	Savinja Golding	0.13	39.2	EU
81	60042	Shinshuwase	0.25	34.5	JAPAN
82	66056	Smooth Cone	0.27	30.3	AUS
83	21702	Sorachi Ace	0.23	43.9	–
84	21187	Southern Brewer	0.22	19.7	AUS
85	21703	Southern Cross	0.23	16.5	–
86	21674	Spalter Select	0.11	54.1	EU
87	21403	Stickelbract	0.23	2.5	AUS
88	21173	Strisselspalter	0.38	24.1	EU
89	21049	Styrian	0.12	51.2	EU
90	21697	Sunbeam	0.21	21.9	USA
91	21281	Sunshine	0.35	17.1	–
92	21405	SuperAlpha	0.14	15.3	AUS
93	65101	Talisman	0.23	18.2	USA
94	21169	Tardif d'Bourgogne	0.46	47.1	EU
95	61021	Tettnanger	0.34	29.4	EU
96	21497	Tettnanger B	0.42	46.7	EU
97	21396	Tolhurst	0.03	23.9	UK
98	21676	Toyomidori	0.38	22.3	JAPAN
99	21484	Ultra	0.13	13.8	–
100	21083	Vojvodina	0.41	36.3	EU
101	21668	Whitbread's Golding	0.18	25.6	UK
102	21041	Willamette	0.15	23.3	USA
103	21043	Wye Challenger	0.04	43.6	UK
104	21044	Wye Northdown	0.07	35.3	UK
105	21282	Wye Saxon	0.28	37.7	UK
106	21112	Wye Target v.f.	0.31	19.9	UK
107	21283	Wye Viking	0.02	36.5	UK
108	21498	Yeoman	0.04	54.5	UK
109	61019	Yugoslavia Golding	0.07	43.7	–
110	21499	Zenith	0.05	14.0	–

[x] US Department of Agriculture accession number.

[y] Plants died during the course of the study; omitted from the analysis.

[z] Origin designations from Henning et al. (2004a): UK = United Kingdom; EU = Continental Europe; USA = United States of America; JAPAN = Japan/Asia; AUS = Australia/New Zealand/former British Commonwealth countries.

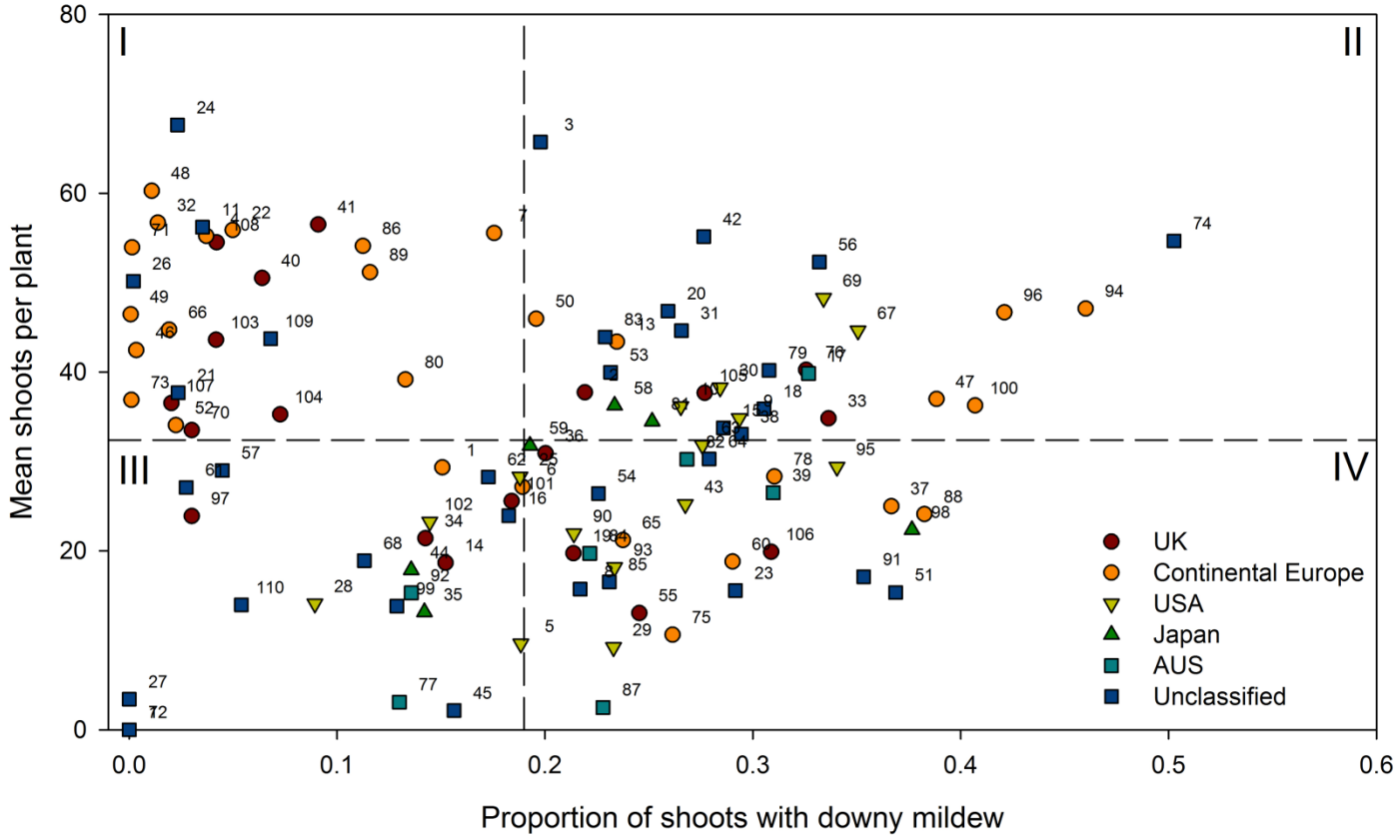

FIGURE 1

Proportion of shoots with downy mildew and mean shoots per plant for each hop cultivar evaluated in Corvallis, Oregon from 2005 to 2007. Legend refers to region of origin as delineated by cluster analysis in Henning et al. (2004a), where Japan indicates Japan and Asia and AUS indicates Australia, New Zealand, and former British Commonwealth countries. Cultivars that were not included in that analysis are dubbed unclassified herein. See Table 1 for reference numbers for each cultivar. The four quadrants in the figure are delineated by the dashed lines representing the overall mean among cultivars for proportion of shoots with downy mildew and total shoots per plant.

with poor disease resistance or low vigor (for whatever reason) are undesirable. Further, conducting these assessments on established plants in the same location over a period of three years reduces the likelihood that a cultivar would escape infection if susceptible and also captures potential decline in vigor over time due to crown infection.

ORIGIN AND CORRELATION WITH CHEMICAL PROPERTIES AND YIELD

Henning et al. (2004a) previously identified five clusters of hop diversity on the basis of yield and chemical characteristics of cones, and these diversity groups were largely related to region of origin, namely United Kingdom, Continental Europe, United States, Japan, and former British Commonwealth countries (e.g., Australia and New Zealand). Seventy-nine cultivars were included in the prior analysis by Henning et al. (2004a) that were also assessed for downy mildew susceptibility and shoot production in this study (Table 2). Utilizing the groups identified by Henning et al. (2004a), differences in downy mildew susceptibility and the total number of shoots produced amongst groups were analyzed in a mixed model considering diversity group as a fixed factor and year as a random factor. Analyses were again carried out using the GLIMMIX procedure in SAS version 9.2 (SAS Institute Inc., Cary, NC) assuming a normal distribution of the response variable after inspection of standard residual diagnostics.

There were significant differences for both downy mildew susceptibility and shoot production among the groups. The cultivars originating from the United Kingdom and Continental Europe had less downy mildew and were more vigorous than those from the United States, Japan, and Australia/New Zealand as indicated by pairwise contrasts ($P = 0.005$; $P < 0.001$, respectively). The region of origin of cultivars in Figure 1 also was summarized by disease phenotype and vigor amongst the four quadrants. In the quadrant in the upper left-hand corner, representing the cultivars with the greatest levels of downy mildew resistance and vigor, all 18 cultivars with known diversity

TABLE 2
Mean incidence of hop shoots with downy mildew and number of shoots produced per plant for 79 hop cultivars grouped within a region of origin.

Origin[x]	Shoots with downy mildew (proportion)	Shoots per plant
United States	0.232 a[y]	30.0 b
Australia/New Zealand	0.204 ab	19.3 c
Japan	0.197 ab	26.7 bc
United Kingdom	0.143 b	32.4 b
Continental Europe	0.142 b	40.2 a

[x] Origin determined by cluster analysis of phenotypic data from Henning et al. (2004a).
[y] Values with the same letters are not statistically different ($P > 0.05$) based on a mixed model analysis.

group originated from the United Kingdom and continental Europe.

Henning et al. (2004a) also reported yield and various chemical properties associated with brewing quality for world hop cultivars. Again, 79 of the cultivars included in the previously published study also were included in the downy mildew assessments reported here. The chemical properties that were evaluated were bittering acids (α- and β-acid content), percent cohumulone of α-acids, stability of bittering acids as measured by the hop storage index, and percent myrcene, caryophyllene, and humulene in the essential oil extracts from the cones (Henning et al. 2004a). The correlation between these chemical measurements and downy mildew susceptibility and shoot production was conducted using the CORR procedure in SAS. Downy mildew susceptibility and shoot production were independent of yield and chemical properties, with the exception of a significant ($P = 0.001$) negative correlation between shoot production and cohumulone levels in the cones (Table 3).

To further establish the association between cohumulone levels and resistance to downy mildew, historical chemistry data (Henning et al. 2004a) was compared amongst cultivars groups in the four quadrants in Figure 1. A mixed model analysis was conducted to test whether there was an association between levels of cohumulone and downy mildew phenotype based on the four quadrants. Quadrant group was considered a fixed, categorical factor in the analysis, and cultivar nested within quadrant group was a random factor. Analyses were again conducted using the GLIMMIX procedure in SAS assuming a normal distribution of the response variable. Cultivars in the upper left-hand quadrant had significantly ($P = 0.05$) lower levels of cohumulone (26.4%) as compared to cultivars in the lower left-hand (33.8%) and right-hand (32.0%) quadrant, thus further confirming a correlation between disease phenotype and this compound.

DISCUSSION AND RECOMMENDATIONS

There is a large range of downy mildew susceptibility and vigor amongst commercial hop cultivars, and some cultivars possess a very high level of resistance. The highest levels of vigor and resistance to shoot infection are associated with cultivars originating from Europe. Disease resistance and vigor were significantly greater in these cultivars as a group than cultivars from the United States, Japan, and Australia/New Zealand. In the absence of downy mildew, cultivars derived from wild North American germplasm generally tend to be higher yielding than cultivars from Europe (Henning et al. 2004a). Vigor measured in the present study was based on the number of shoots per plant, and not yield. Nonetheless, the generally poor vigor observed in cultivars derived outside of Europe likely is indicative of a lack of tolerance to the crown infection phase of the disease and a consequent decline in shoot production.

The negative correlation between cohumulone and the number of shoots produced per plant may indicate a general susceptibility of North American germplasm to downy mildew. Cohumulone is a component of the α-acids and can impart an undesirable harshness to beer, and high levels of cohumuluone often are selected against in breeding programs (Neve 1991; Haunold et al. 1993). Cohumulone levels tend to be greatest in germplasm derived from North America (Haunold et al. 1993; Henning 2004a). Thus, the negative correlation between the number of shoots produced per plant and level of cohumulone might further indicate a general lack of tolerance to downy mildew in cultivars with wild North American ancestry and/or linkage between these traits. The correlation analyses are further supported by analysis of chemical data amongst the four classes of disease/vigor phenotype identified herein (Fig. 1).

Breeding efforts face the challenge of incorporating disease resistance while maintaining desirable brewing characteristics and agronomic traits (Skotland and Johnson 1983; Neve 1991; Parker 2007). Because of the nature of breeding for a quantitative trait like downy mildew resistance, breeding success has been slow, as witnessed in the decades invested in developing cultivars like Perle and Hueller Bitterer, which possess among the highest levels of resistance (Neve 1991). Progress in breeding for resistance might be accelerated if new sources of resistant germplasm can be identified.

Wild germplasm from North America may not have been exposed to *P. humuli* since the migration of hop from Japan and southern China to North America (Murakami et al. 2006). This may explain the reported greater susceptibility of cultivars that originate from North America germplasm (Neve 1991; Haunold et al. 1993; Mancino 2013). Nonetheless, North American germplasm is highly diverse and a valuable source of high yield, high levels of α-acids, and unique aromas (Haunold et al. 1993; Hampton et al. 2001; Murakami et al. 2006). Attempting to combine downy mildew resistance with these agronomic traits is difficult, as the best source of disease resistance seems to be found in cultivars from the United Kingdom and Europe, which typically are low yielding (Henning et al. 2004a) and often lack distinctive aroma and flavor characteristics that are currently desired by craft brewers. Incorporating downy mildew resistance, appropriate agronomic characteristics, and aroma and flavor profiles desired by brewers is thus a long-term endeavor. Recently, quantitative trait loci (QTL) markers have been identified for downy mildew resistance that could be used to make marker-assisted selections for resistance and expedite identification of progeny with higher levels of resistance (Henning et al. 2015).

Although cultivars derived in Europe tended to be least susceptible to downy mildew, this may be due to more active selection for downy mildew resistance in breeding programs rather than inherent differences in native germplasm. Given that the center of origin of the genus *Humulus* and *P. humuli* is thought to be China (Murakami et al. 2006), wild hops and germplasm from southeast Asia might be a new source of downy

TABLE 3
Spearman's rank correlation coefficient (S) for proportion of shoots with downy mildew and mean shoots per plant with yield and seven chemical properties for 79 hop cultivars.

Variable	Yield	α -acids	β -acids	HSI[x]	CoH	M	C	H
Proportion of shoots with downy mildew	0.13	–0.11	0.13	–0.0022	–0.007	–0.05	–0.05	–0.003
Mean shoots	–0.05	0.05	0.11	–0.02	–0.37*	0.06	–0.01	0.05

[x] Hop Storage Index (HSI), Cohumulone percentage (CoH), Myrcene concentration (M), Caryophyllene concentration (C), Humulene concentration (H) as reported in Henning et al. (2004a).

* Asterisk indicates a significant correlation ($P = 0.05$).

mildew resistance, and evaluation of germplasm from this region is warranted. Further, the Japanese hop, *Humulus japonicus*, an ancestor of *H. lupulus* and indigenous to southeast Asia, is almost entirely resistant to hop downy mildew (Hoerner 1940). Recent studies conducted by Mancino (2013) found only one instance where a sporangiophore of *P. humuli* developed on *H. japonicus. Humulus japonicus* was immune to *P. cubensis* as well (Mancino 2013). It is possible that *H. japonicus* may be a genetic source of resistance that could be valuable for introgression into hop, although hybridization of *H. japonicus* and *H. lupulus* may not be possible (Hoerner 1940).

Breeding for downy mildew resistance requires basic information of susceptibility of potential parents, as well as their genetic relatedness because of heterotic potential in hop for certain traits (Henning et al. 2004b). These data provide disease susceptibility and vigor information for 110 world hop cultivars, and demonstrate that downy mildew resistance is associated with cultivars from the United Kingdom and continental Europe. The narrow genetic base of cultivars with high levels of resistance to the disease is problematic. Efforts to introgress new sources of downy mildew resistance into North American germplasm are needed immediately.

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