Introduction

Many agricultural crops and wild plants require pollination in order to reproduce. This pollination service is often provided by insect floral visitors, particularly bees. A number of plants, both in agricultural and natural settings, are so dependent on insect-vectored pollination that they are incapable of reproduction without it (McGregor, Levin and Foster, 1965; Nilsson, 1992; Ortega et al., 2002).

The domestic cranberry (*Vaccinium macrocarpon* Aiton [Ericaceae]) is a low-lying, vining, perennial shrub native to northeastern North America. Fruit set and fruit size are maximized when 8 or more pollen tetrads are transferred to the stigma of the flower; without sufficient pollination, fruit are small, deformed or altogether absent (Cane and Schiffhauer, 2003). Because of its poor self-compatibility, cranberry requires insect pollinators to set fruit. *Apis mellifera*, the European honeybee, is used extensively to provide pollination services for most fruit and vegetable crops, including cranberry. However, the number of available hives has decreased with recent threats to honeybee health such as Colony Collapse Disorder, mites and other diseases. In order to mitigate losses in pollination services, native bees are being evaluated as alternative pollinators in many agricultural systems (Winfree et al., 2007).

Previous cranberry pollination research has focused on the Great Lakes and New England areas and has primarily used commercially available bee species: honeybees, domesticated bumble bees (*Bombus* spp.), leafcutter bees (*Megachile* spp.), and mason bees (*Osmia* spp.). In these studies, bumble bees have proven to be effective pollinators of cranberries because their large size and pollen collecting devices allow

them to deposit many pollen grains on the flower stigma with each visit (Macfarlane, 1995). It has also been noted that honeybees are more likely than bumble bees to extract cranberry nectar without providing pollination services (MacKenzie, 1994). However, very little research has been done on cranberry production systems in the West, which produces approximately 16% of the cranberries in North America (BC Cranberry Growers Assoc., 2007; USDA, 2009). Oregon produces 4% of North American cranberries, worth $36.6 million (USDA, 2009), on relatively little acreage on the southern portion of its coast.

Cranberries bloom in Oregon from mid-May to late July. The cool temperatures, overcast skies, high wind and precipitation experienced during this period discourage *A. mellifera* from foraging, which can dramatically reduce pollination services (Percival, 1947; Burrill and Dietz, 1981). Native bees, adapted to coastal conditions, have the potential to be superior pollinators. There is little information on which of the approximately 400 bee species native to Oregon are present in the cranberry producing areas along the southern coast or if any of the species present are associated with cranberry bloom.

This lack of information is, in part, due to the absence of an effective passive sampling device. Recent research at Oregon State University indicates that blue vane traps are attractive to a multitude of bee species (Apoidiae) and may be used to monitor them (Fig. 1; Stephen and Rao 2005). Use of the blue vane trap makes it possible to sample a large area with relatively little manpower, enabling the study of native bee species across the cranberry growing region of southwestern coastal Oregon.

The objectives of this study were 1) to estimate native bee diversity and

abundance in the cranberry growing region of Oregon; 2) to correlate bee foraging behaviors to the abiotic factors of temperature and wind; and 3) to analyze the composition of pollen loads collected from bees working cranberry flowers.

Materials and Methods

Study Sites. The cranberry-growing region of southern coastal Oregon extends from just north of Bandon to just north of Port Orford, a distance of more than 40 km. Because no previous research has been done on the native bee composition of this region, sites were chosen across 22 km of the north-south gradient. Four farm sites were selected and labeled Site 1 through Site 4, with the former being northernmost and the latter being southernmost. Absolute distances between the sites ranged from 4.2 km to 9.8 km. Individual cranberry beds were uniformly 0.5-1.0 hectares at all sites, though the total acreage planted to cranberry varied from 4.5 hectares at Site 1 to over 65 hectares at Site 4. The composition of the area surrounding each site also varied from roadside and pastureland to completely forested (see Appendix A for more information).

Estimation of of Native Bee Diversity and Abundance. Blue vane traps (SpringStar LLC, Woodinville, WA, USA) were used to passively sample bees. Each trap consisted of a clear plastic collection jar (15 cm diameter x 15 cm high) with a funnel cap and two cross-vanes (24 cm tall x 13 cm wide) made of fluorescent blue polypropylene. Traps were hung 10 cm above the ground on rebar posts (Fig. 1) between two cranberry beds and the surrounding environment. Two traps were placed at

each farm site at dawn and collected at dusk (12 hrs later) for a total of eight traps per sampling event. The bees caught in the traps were transferred to paper cups with lids and frozen; they were later thawed, pinned, labeled and identified. Sampling events occurred on Saturdays once every other week before and after cranberry bloom, and once per week during bloom. Seven sampling events occurred between May 15 and July 26 in 2008; nine sampling events occurred between May 16 and July 11 in 2009.

Bee Foraging and Abiotic Factors. To estimate which bees were actively foraging on cranberries, two-minute counts were taken along a transect. Every two hours from 8:00am-2:00pm during sample days in 2008 and every hour from 8:00am-2:00pm during sample days in 2009, bees were counted along an L-shaped transect of the cranberry bed with the harshest weather (Site 4). All foraging bees within 1 m of the transect were visually identified. *Apis mellifera* and *Bombus* spp. were identified to species, other bees were identified to genus or tribe. Before every count, the wind speed and temperature were measured with an anemometer over a 2-minute interval and recorded.

Data were analyzed using R to create binomial logistic regression models for bee foraging behavior. Single-variable regressions were used to determine correlations between wind speed and bee foraging and temperature and bee foraging. A multivariate regression model was also constructed to account for both temperature and wind speed effects on bee presence simultaneously.

Pollen Load Analysis. Pollen was collected from both flowering plants and

foraging bees. Ten to thirty anthers were gathered from 2 - 5 specimens of each plant species observed blooming near any of the 4 sites during the sample period to create a reference collection. Anthers were not collected from some flowering trees due to the difficulty of access. A list of flowering plants at the study sites can be found in Appendix A. Bee collection occurred at Site 4. During sample days, four honeybees and four native bees were collected in vials every two hours if available. Variable weather conditions often prevented the collection of the full number of bees. At the time of collection, the genus, species, date, plant on which foraging and time were recorded. Bees were then chilled in a cooler and their pollen brushed into a labeled vial using a paintbrush. After all pollen was removed from the pollen collecting devices, the bees were released. Pollen samples were frozen and stored for analysis.

Pollen was processed through an acetolysis procedure originally presented by Erdtman (1952), modified by Skyrm (personal communication). Anthers from each plant species were placed in 1.5 mL conical-bottomed centrifuge tubes with 1.0 mL of glacial acetic acid and agitated for 30 seconds. The anthers were removed from each tube with forceps and the tubes were centrifuged at 4000 rpm for 4 minutes. The liquid was decanted and 1.5 mL glacial acetic acid was added to each tube. Tubes were agitated, centrifuged, and decanted a second time. Acetolysis mixture was prepared by combining one part concentrated sulfuric acid with nine parts acetic anhydride; sulfuric acid was added dropwise to the acetic anhydride while stirring with a glass rod. Each centrifuge tube received 1.0 mL of the acetolysis mixture and was placed in a block heater at 100 °C for 3 minutes. Tubes were then removed, centrifuged, and the liquid decanted into running water. Glacial acetic acid was added to fill each tube. Tubes were

agitated, centrifuged, and the liquid decanted. To each centrifuge tube, 1.5 mL of de-ionized water was added. Tubes were agitated, centrifuged, and the liquid decanted. Deionized water was mixed with saffranin-O to create a 0.01% dye solution. Each centrifuge tube received 1.5 mL of dye solution. Tubes were agitated, centrifuged, and half the liquid decanted. The resulting dyed pollen was mounted on slides with silicone oil.

Pollen from bees was dried, weighed and processed in the same way as the anthers (excepting the removal with forceps). The reference collection of pollen from plant samples (Appendix B) was used to inform pollen load analysis. Pollen morphology was used to differentiate individual grains except for pollen from the family Ericaceae. Because Ericaceae pollen tetrads all have similar morphology, size was used to separate cranberry pollen, which was 12.5 - 15.0 μm across (Fig. 4). For each bee pollen sample, 200 grains were identified in longitudinal transects of the slide.

Results

Estimation of of Native Bee Diversity and Abundance. Over the two growing seasons, 1,337 bees were collected, representing five families, thirteen genera, and over 27 species (Table 1). The following genera were trapped in higher abundance than *A. mellifera*: *Bombus*, *Agapostemon*, and *Lasioglossum*.

Bees in the genus *Bombus* (bumble bees), which have previously been shown to be efficient pollinators of cranberries and other members of the family Ericaceae, were observed in high numbers; *Bombus* comprised 25.1% of all bees captured. Five

species of bumble bees were captured including the phenotypically similar *B. caliginosus* Frison and *B. vosnesenskii* (together referred hereafter as *B. vosnesenskii*), *B. mixtus* Cresson, *B. melanopygus* Nylander, and *B. californicus* Smith. The most abundant was the western yellow-faced bee, *B. vosnesenskii*, which constituted 50.1% of all bumble bees.

Two species of *Agapostemon* were trapped: *A. texanus* Cresson and *A. virescens* Fabricius. *Agapostemon texanus*, a completely metallic green sweat bee, was particularly abundant, comprising 24.6% of all bees captured and 98.5% of all *Agapostemon*.

Agapostemon texanus, *B. vosnesenskii*, and the bees in the *Lasioglossum* complex all seem to be present when cranberries were blooming (Fig. 2). However, as the *Lasioglossum* complex contains at least six species which were not separated in this study, it was impossible to determine the utility of any individual species.

Bee Foraging and Abiotic Factors. During the two-minute counts, *A. mellifera* and *Bombus* spp. were the dominant bee species observed foraging on the beds (99.7% of total). Honeybees accounted for 69.0% of the observed cranberry pollinators, bumble bees 30.7%. The bumble bees observed foraging were largely *B. vosnesenskii* (70.8%), the remainder were *B. mixtus* (22.9%) and *B. melanopygus* (6.3%). Over the study period, a small number of halictid bees were also observed foraging on cranberry, but their contribution to pollination is likely to be insignificant due to their extremely low abundance. A total of 207 honeybees and 96 bumble bees were observed foraging.

We examined the correlation between temperature, wind speed and foraging

bees. Temperature was highly correlated with bee foragers (P<0.0001; Fig. 3). The interquartile range (middle 50%) of *Bombus* foraging was 18.3 - 22.2 °C, while the interquartile range of *A. mellifera* foraging was 21.1 - 26.7 °C. There was no statistical difference between honeybee and bumble bee forager activity due to wind speed alone (P=0.104).

Because wind speed increased in the middle of the day, when temperatures typically were increasing, these variables were not independent. It is possible that in the single-variable models above, temperature was acting as a confounding factor for analyzing the effect of wind. When temperature and wind speed were considered together, both were significant predictors of bee foragers (P<0.0001 and P=0.0012, respectively; Table 2). For every 1 °C increase in temperature, the odds of sighting a foraging honeybee (versus a bumble bee) increase by a factor of 1.37; for every 1 m/s increase in wind speed, the odds of sighting a foraging honeybee increase by a factor of 1.04. The average observed temperature during counts was 19.5 °C from mid-May to late July. Honeybees reached their highest numbers when temperatures exceeded 24 °C, an event that occurred during less than 20% of observations over the study period.

Pollen Analysis. Of the bees collected for pollen analysis, 62.8% of honeybees and 88.7% of bumble bees were carrying pollen. The average nonzero dry weight of a honeybee pollen load was 1.7 ± 0.3 mg, while a bumble bee pollen load was 6.6 ± 0.9 mg. Both honeybees and bumble bees were observed to have mixed loads. For *A. mellifera*, mixed loads contained 89.4% cranberry pollen on average with 1-3 other pollen types comprising the remainder. For *Bombus* species, mixed loads contained

82.0% cranberry pollen on average with 1-5 other pollen types comprising the remainder. The most common contaminant was pollen from weedy Fabaceae (7.1% of all pollen). Other major contaminants belonged to the families Asteraceae (2.4%), Ranunculaceae (1.2%) and Rhamnaceae (0.9%). Both *A. mellifera* and *Bombus* spp. foragers collected pollen loads which, on average, contained 82-97% cranberry pollen. No statistical difference was observed in pollen load composition between the two genera.

Discussion

Of at least 27 bee species observed in the cranberry growing region of Oregon, four appear to play a role in cranberry pollination: *A. mellifera*, *B. vosnesenskii*, *B. mixtus*, and *B. melanopygus*. While other genera were common in the traps, they were not observed foraging on cranberry bloom and may have instead been utilizing plants in the surrounding landscape with bloom concurrent to cranberry. It is possible that these plants are competing with cranberry for pollinators.

Honeybees accounted for 69.0% of the observed cranberry pollinators, bumble bees 30.7%, and other bees 0.3%. Despite their higher numbers, honeybees may not be providing greater pollination services than bumble bees. Other studies have shown that bees in the genus *Bombus* foraging on cranberry deposit as much as six times the amount of pollen as honeybees per visit, significantly increasing yield (Cane and Schiffhauer, 2003). In addition, honeybees are known nectar-robbers of cranberry (MacKenzie, 1994). In this study, honeybees were observed collecting nectar but no

pollen significantly more often than bumble bees; 37.2% of honeybees and only 11.3% of bumble bees working flowers had empty pollen collecting devices. *B. vosnesenskii* constituted 73.9% of bumble bees, and 22.7% of the total observations, and is likely to be the most important native pollinator of cranberry.

Data from pollen collection must be tempered with observations of actual foraging habits. As previously mentioned, honeybees have a high instance of collecting nectar without collecting pollen, but they also have abiotic limitations to their foraging potential. For every 1 °C increase in temperature, the odds of sighting a foraging honeybee (versus a bumble bee) increased by a factor of 1.37. Half of the observed honeybees foraged between 21.1 and 26.7 °C. Over 75% of honeybees were seen foraging above the average observed temperature (19.5 °C), indicating that honeybees prefer to forage at temperatures above what are generally present during cranberry bloom. While honeybee sightings do slightly increase with wind speed, this is probably because the bees were grounded at wind speeds above 45 m/s and were observed crawling through the mat of cranberries. Bumble bees, on the other hand, largely forage between 18.3 and 22.2 °C, which brackets the observed average daytime temperature. *B. vosnesenskii* was even observed flying from cranberry flower to cranberry flower at wind speeds above 55 m/s.

Pollen analysis showed that for both *A. mellifera* and *Bombus* spp., foragers largely collected cranberry pollen, which comprised 82-97% of pollen loads. There was no statistical difference in composition of pollen loads between the two genera. Both honeybees and bumble bees were found to have mixed loads; the most common contaminant was pollen from weedy legume species. Because contamination was low,

we can infer that, when honeybees and bumble bees are collecting pollen, they are more likely to go from cranberry flower to cranberry flower than switch to weedy species.

The major limitation of the observational component of this study is that bees were only observed until 2:00pm, when the afternoon winds picked up, and only at one location. While there were few bees out at this time, it is possible that they began foraging again before dusk and were not counted. However, the data presently collected strongly indicate that bumble bees in general and *B. vosnesenskii* in particular play a significant role in cranberry pollination in Oregon. Bumble bees have previously been found to be excellent pollinators of cranberries in the Midwest (MacKenzie et al., 1995; Cane and Schiffhauer, 2003) and their importance is underscored in this study. It may be possible to reduce dependence on honeybees by carefully managing habitat to maintain present wild bumble bee populations. In the future, managed colonies of native bees may also provide these services, not just for cranberries, but for many agricultural crops.

Table 1. Diversity of bee fauna trapped in Oregon cranberry from 2008 – 2009.

Family	Genus	Species	S1	S2	S3	S4	Species Total	Genus Total
Andrenidae	*Andrena*	spp. (2)	1	1	7	1	10	10
Apidae	*Apis*	*mellifera*	110	58	12	57	237	237
	Bombus	*californicus*	1	0	2	1	4	-
	Bombus	*melanopygus*	29	9	0	22	60	-
	Bombus	*mixtus*	65	21	0	16	102	-
	Bombus	*vosnesenskii**	56	40	6	88	190	356
	Ceratina	sp.	0	0	1	0	1	1
	Melissodes	spp. (3+)	2	6	28	21	57	57
	Synhalonia	spp. (1+)	1	2	0	1	4	4
Colletidae	*Colletes*	sp.	1	0	0	2	3	3
Halictidae	*Agapostemon*	*texanus*	81	126	35	82	324	-
	Agapostemon	*virescens*	1	0	1	3	5	329
	Halictus	*rubicundus*	17	2	1	10	30	30
	Lasioglossum	spp. (6+)	72	92	17	58	239	239
	Lasioglossum	*olympiae*	1	0	0	2	3	-
	Lasioglossum	*pacificum*	12	11	8	14	45	-
	Lasioglossum	*sysimbrium*	1	1	1	0	3	51
	Nomada	sp.	1	0	0	0	1	1
Megachilidae	*Megachile*	spp. (1+)	2	8	3	3	16	16
	Osmia	spp. (1+)	2	1	0	0	3	3
		Total	456	378	122	381	1337	

* Including *B. caliginosis*

Table 2. Multivariate logistic model associating honeybee and bumble bee foraging to abiotic factors. Both temperature and wind speed are predictive of bee foraging. Residual deviance is 308.19 on 297 degrees of freedom. AIC is 314.19.

	Estimate	Std. Error	z value	Pr (>|z|)
(Intercept)	-7.03161	1.13961	-6.170	6.82×10^{-10} ***
Temperature (C)	0.31453	0.04745	6.629	3.38×10^{-11} ***
Wind speed (m/s)	0.03997	0.01234	3.238	0.00120 **

** $P > 0.01$
*** $P > 0.001$

Fig. 1. Fluorescent blue vane trap used for assessment of native bee biodiversity.

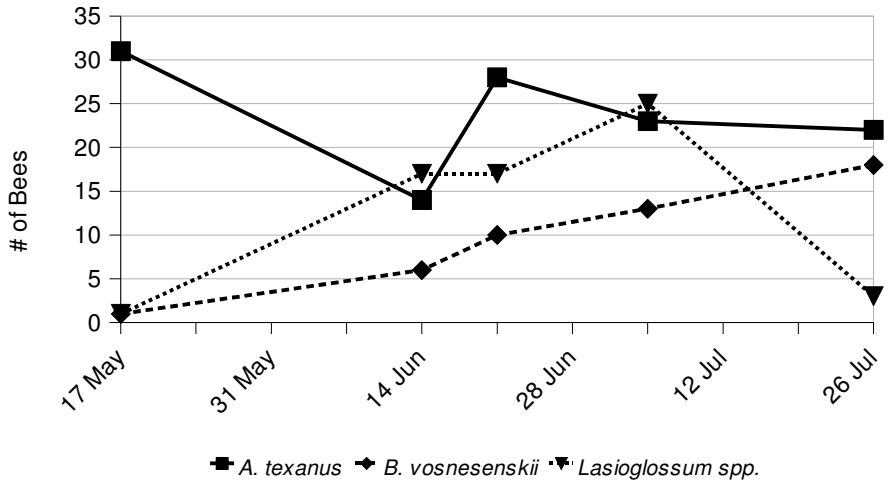

Fig. 2. Seasonal presence of common native bee genera across four Oregon cranberry sites in 2008.

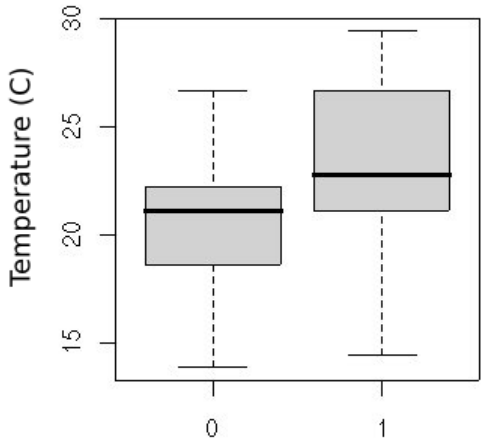

Fig. 3. Distribution of bee foragers with respect to temperature. A value of 1 corresponds to the presence of a bumble bee, 0 corresponds to a honeybee. Distributions were compared using a binomial logistic model and found to be significantly different ($P < 0.0001$).

Fig. 4: Pollen grains from the family Ericaceae. From left to right: *Rhododendron groenlandicum* (bog Labrador tea), *Vaccinium macrocarpon* (cranberry), *Arctostaphylos* sp. (manzinita), *Gaultheria shallon* (salal), and *Rhododendron* sp (rhododendron).

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APPENDIX A

Site Descriptions

Sampled: 5/17/08, 5/31/08, 6/14/08, 6/21/08, 6/28/08, 7/5/08, 7/26/08
5/16/09, 5/23/09, 5/30/09, 6/6/09, 6/13/09, 6/20/09, 6/27/09, 6/30/09, 7/4/09, 7/11/09

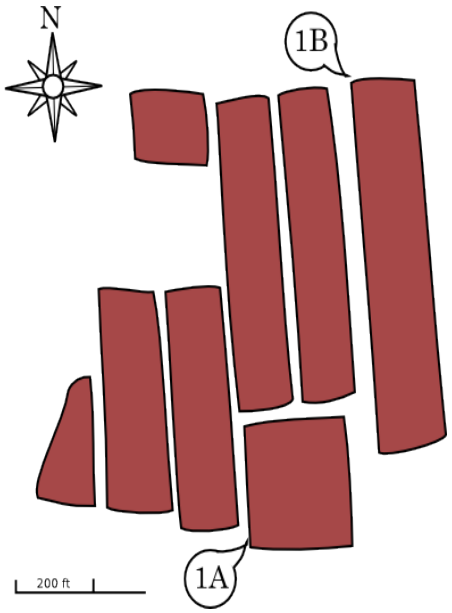
Sites: Site 1: Bandon, OR
Surrounded by forested area on all sides interspersed with small residential properties. 9.8 km north of Site 2.

Site 2: Langlois, OR
Surrounded by other cranberry beds, forest and pastureland. 8.7 km northeast of Site 3.

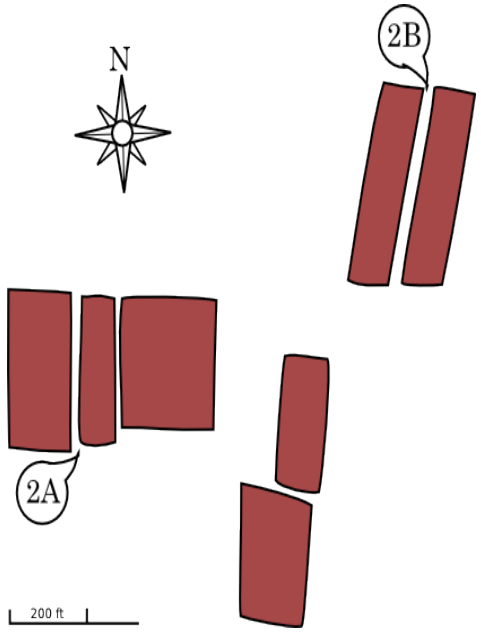
Site 3: Langlois, OR
Surrounded by pasture on three sides, with highway on the fourth. Situated on a west-facing hill which is forested after ~200m of pasture. 4.2 km northeast of Site 4.

Site 4: Sixes, OR
Surrounded by forested area on all sides. Forest is owned by grower and covers over 800 ha.

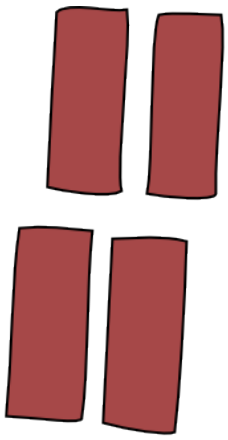
Traps: 1A, 1B, 2A, 2B, 3A, 3B, 4A, 4B

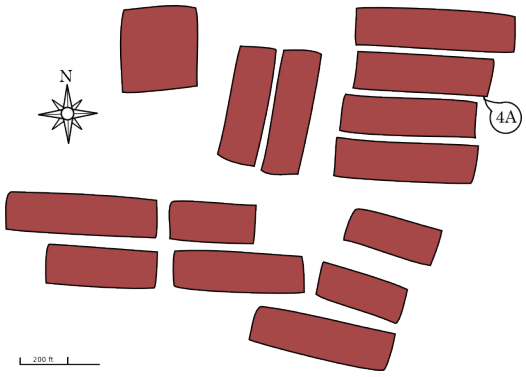


trap 1A: 43.05N, 124.40W GPS
trap 1B: 43.06N, 124.40W GPS

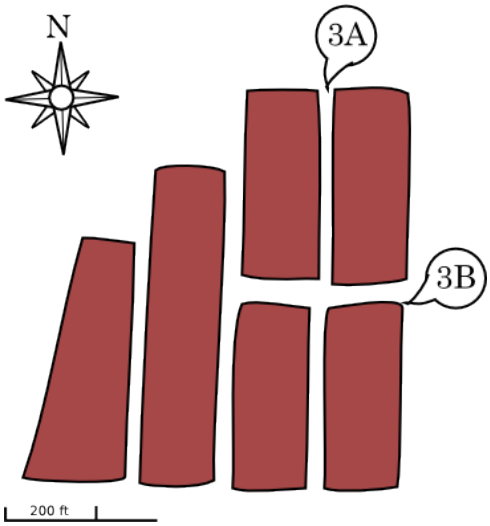


trap 2A: 42.97N, 124.43W
trap 2B: 42.97N, 124.43W

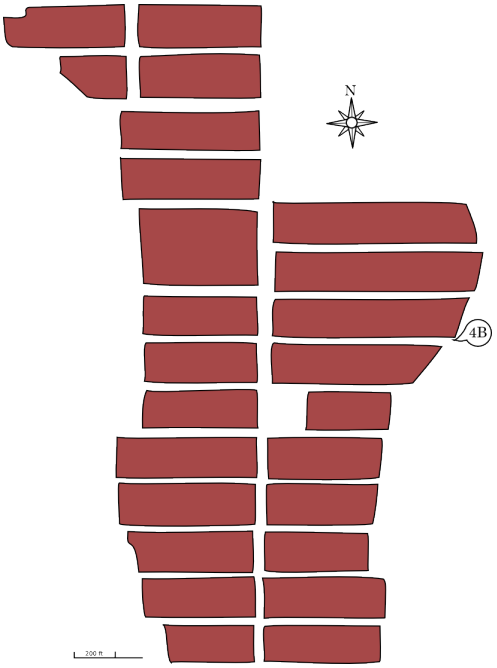




trap 4A: 42.88N, 124.48W



trap 3A: 42.90N, 124.46W GPS
trap 3B: 42.90N, 124.46W GPS



trap 4B: 42.87N, 124.49W

Flowering Plants in Vicinity of Sample Sites

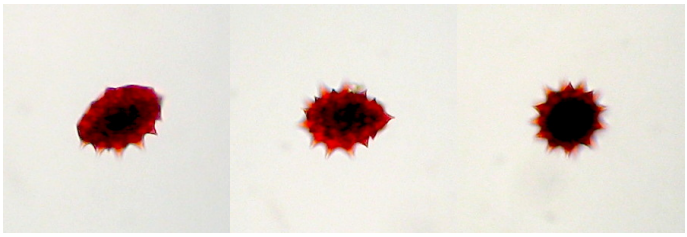
Family	Scientific Name	Common Name
Asteraceae	*Aster*	purple aster
	Bellis perennis	English daisy
	Hypochaeris radicata	false dandelion
	Taraxacum	dandelion

Boraginaceae	*Myosotis discolor*	changing forget-me-not
Caprifoliaceae	*Lanicera involucrata*	twinberry
Caryophyllaceae	*Cerastium*	chickweed
Ericaceae	*Arbutus*	madrona
	Arctostaphylos	manzanita
	Erica lusitanica	Spanish heath
	Gaultheria shallon	salal
	Rhododendron	rhododendron
	Rhododendron groenlandicum	bog Labrador tea
	Vaccinium macrocarpon	cranberry
	Vaccinium ovatum	evergreen huckleberry
	Vaccinium sp.	huckleberry
Fabaceae	*Lotus*	lotus
	Lupinus	lupine
	Sarothamnus scoparius	Scotch broom
	Trifolium	clover
	Trifolium dubium	least hop clover
	Trifolium subterranium	subterranean clover
	Ulex europaeus	gorse
	Vicia	vetch
Grossulariaceae	*Ribes*	wild currant
Iridaceae	*Iris*	wild iris
Liliaceae	*Lilium columbianum*	Columbia lily
Linaceae	*Linum bienne*	European flax
Myrtaceae	*Eucalyptus*	eucalyptus
Orobanchaceae	*Boschniakia hookeri*	ground cone
	Euphrasia	eyebright
Plantaginaceae	*Digitalis*	foxglove
	Plantago lanceolata	buckhorn plantain
Polygonaceae	*Rumex acetosella*	sheep sorrel
Portulacaceae	*Claytonia perfoliata*	miner's lettuce
Ranunculaceae	*Ranunculus*	buttercup
Rhamnaceae	*Rhamnus purshiana*	cascara
Rosaceae	*Potentilla*	cinquefoil
	Pyrus	pear
	Rubus armeniacus	Himalayan blackberry
	Rubus parviflorus	thimbleberry
	Rubus spectabilis	salmonberry
	Rubus ursinus	Pacific blackberry

APPENDIX B

Pollen Reference Collection

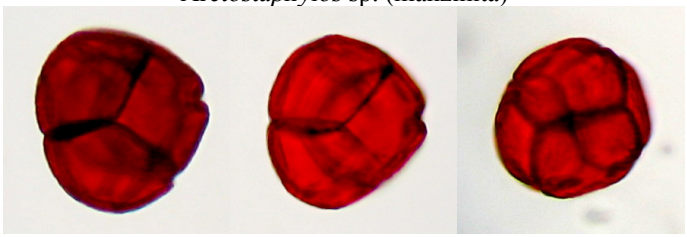
ASTERACEAE



Unknowns

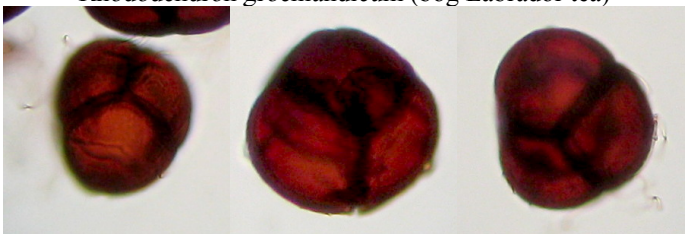
ERICACEAE

Arctostaphylos sp. (manzinita)

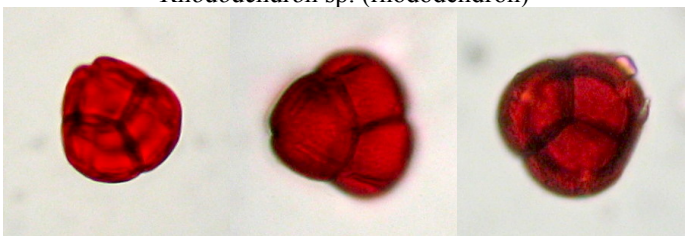


Gaultheria shallon (salal)

Rhododendron groenlandicum (bog Labrador tea)

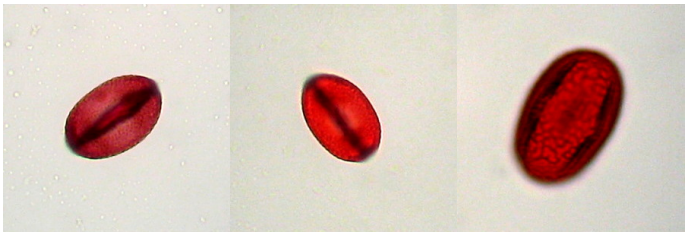


Rhododendron sp. (rhododendron)

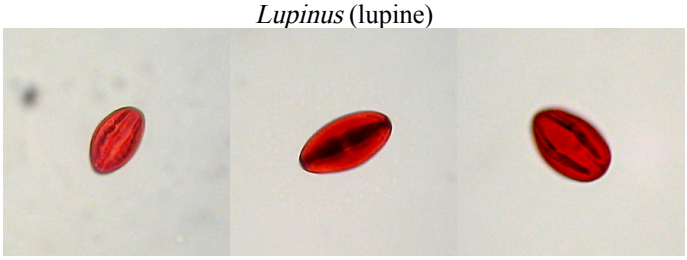


Vaccinium macrocarpon (cranberry)

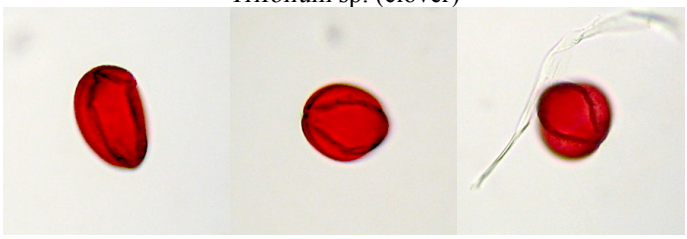
FABACEAE



Lupinus (lupine)

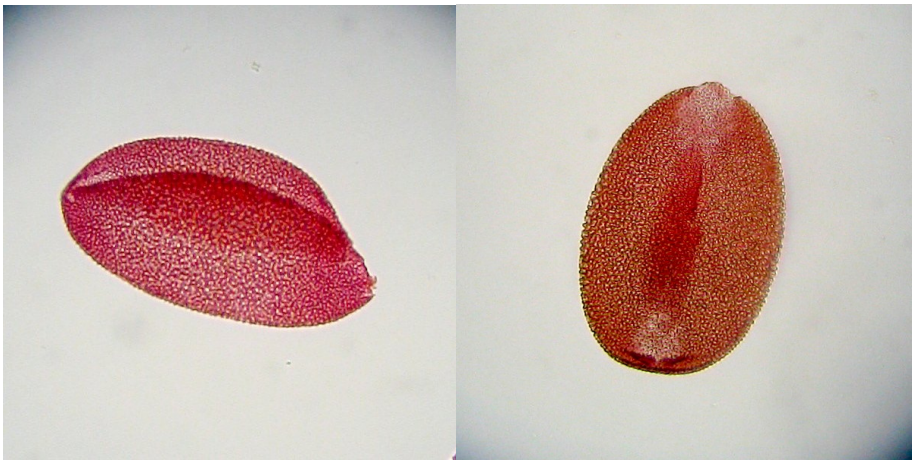


Trifolium sp. (clover)



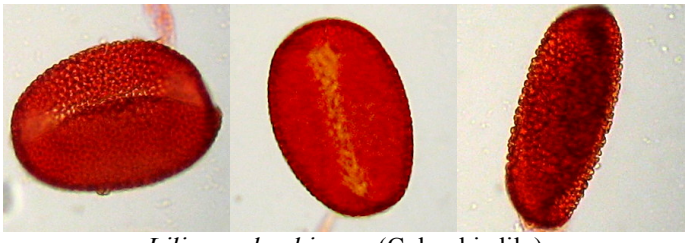
Ulex europaeus (gorse)

IRIDACEAE



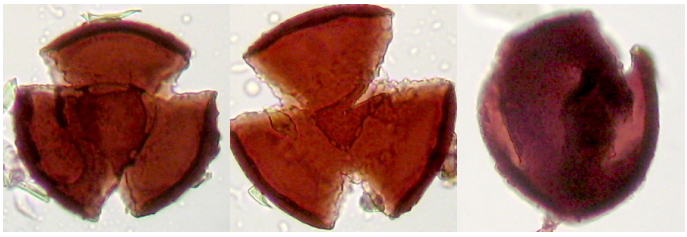
Iris tenax (wild iris)

LILIACEAE



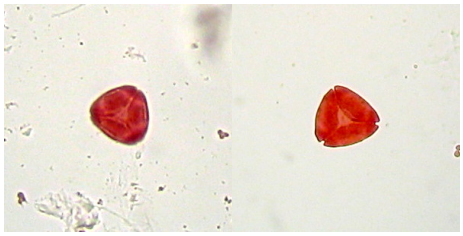
Lilium columbianum (Columbia lily)

LINACEAE



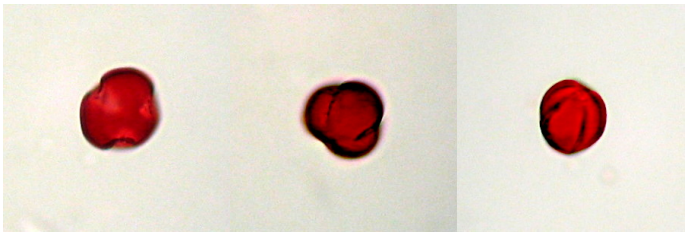
Linum bienne (biennial flax)

MYRTACEAE



Eucalyptus (eucalyptus)

OROBANCHACEAE



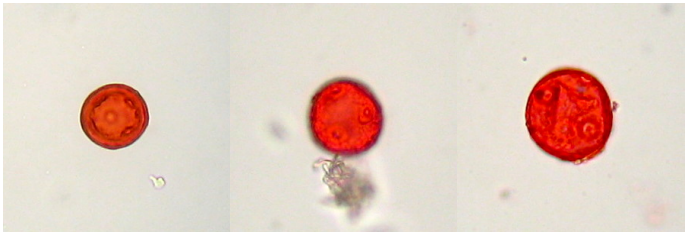
Boschniakia hookeri (ground cone)

PINACEAE

Unknown

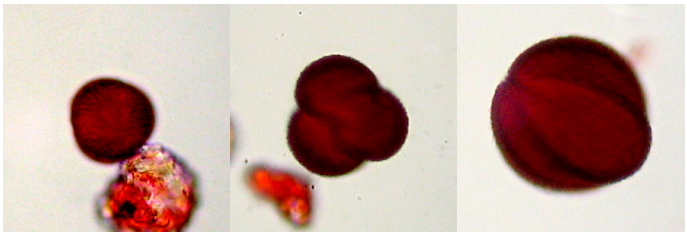
PLANTAGINACEAE

Digitalis sp. (foxglove)



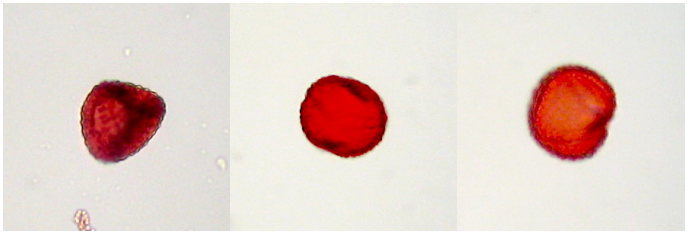
Plantago lanceolata (buckhorn plantain)

PORTULACACEAE



Claytonia perfoliata (miner's lettuce)

RANUNCULACEAE

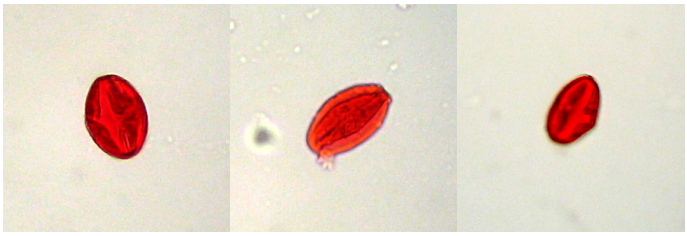


Ranunculus sp. (buttercup)

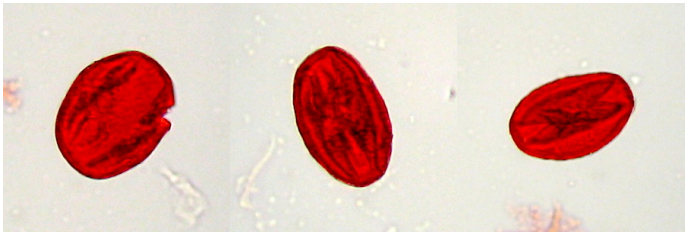
RHAMNACEAE

Rhamnus purshiana (cascara)

ROSACEAE



Rubus parviflorus (thimbleberry)



Rubus ursinus (Pacific blackberry)

APPENDIX C

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