Title

Aboveground spatial variation of arthropod biomass and diversity along gradients of plant biomass and net primary productivity at Wild Basin Wilderness Preserve, Austin TX.

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Abstract

The production of forests -both their standing crops of biomass and growth rates of such biomass- is universally underestimated, as research favors measuring primary (plant) production while neglecting consumer production. Consumer (including herbivore) production is a non-negligible component of primary production because averaged over time, consumer production in a closed ecosystem only results from energy drawn from plant production.

Forest production estimates will be improved and increased by including the component of animal production. Determining the covariation of consumer production with plant production is crucial to understand forest energy (=carbon) storage and flows. A strong positive relationship between consumer and plant production while controlling for environmental variability is expected. Consumer production may co-vary with plant production so closely that simple invertebrate sampling can be used to accurately estimate plant production in forests.

Finding higher production values of forests by including consumer production will increase estimates of carbon sequestration by such forests, implying increased priority for conservation.

Introduction

Definitions:

Biomass: the energy content of organisms per unit area.
Productivity: biomass per unit time.
Production: for convenience, this paper uses production *only* when referring to *both* biomass and biomass per unit time, using producti*vity* to distinguish the latter alone.
Net primary productivity (NPP): plant (and other producer) productivity not respired.

Globally, production estimates of forests are systematically underestimated because production measurement is biased towards wood while huge losses to consumers such as animals are neglected (Roy et al. 2001, Clark et al. 2001). Accurately measured animal production data can be used to estimate these losses to consumers (Petrusewicz. 1967). If exacting quantification methods are used, and environmental variability is controlled, a forest's animal production may show consistently predictable covariance along plant production gradients, allowing estimation of animal production as a function of plant production.

Forest NPP encompasses new growth, litterfall, leachates, volatiles, mortality, and losses to herbivory (Clark et al. 2001, Fahey and Knapp 2007). However, studies of forest NPP mostly measure new wood and litterfall, ignoring herbivory or other consumer losses (Roy et al. 2001, Clark et al. 2001). When herbivory *is* measured, most studies consider only leaf-chewing herbivore guilds because methods of measuring and simulating leaf area loss are well established (Clark et al. 2001, Basset et al. 2003, Lowman and Rinker 2004, Zvereva et al. 2010). Studies measuring production of non-herbivore consumers such as detritovores are yet more rare (Clark et al. 2001).

Studies measuring herbivore production largely consider folivores (leaf-eaters) because methods of measuring and simulating leaf area loss are well established (Clark et al. 2001, Lowman and Rinker 2004). Leaf-chewers may typically eat 10-30% of a tree's leaf production but the amount eaten by sap-feeders or other herbivore feeding guilds is more uncertain (Lowman and Rinker 2004, Zvereva et al 2010). A recent review suggests sap-feeders may use more carbon and nutrients than leaf-chewers and alone reduce woody plant growth by 29% (Zvereva et al 2010). Dixon (1971) found aphid-excluded lime trees had 200% greater wood production than aphid-infested ones. Karban (1982) found significantly higher wood production in trees physically excluded from cicadas. Crawley (1985) demonstrated insecticidal reduction of herbivory on oaks increased acorn production.

Clearly herbivores are an important, but often neglected, component of forest production. The energetic role of non-herbivore consumers in forest production is virtually entirely ignored by the literature. In addition to applying standard NPP measurements, this study applies novel consumer production measurements, thereby increasing estimates of forest production.

In most general terms, this study asks the following question: how does consumer production co-vary with primary production in forest ecosystems? More specifically, this study asks: in central TX forests, controlling for variability in the abiotic environment, from scales spanning the individual tree to its resident grove to its local topographic forest type, how do scientifically estimated quantities of aboveground plant biomass and productivity co-vary with aboveground arthropod biomass and productivity?

Hypotheses: The greater the biomass and productivity of plants at all scales (tree, grove, and forest type), canopy arthropods will exhibit higher than expected 1) alpha and beta diversity, both a) taxonomically and b) by feeding guild / trophic level; 2) total and average per feeding guild biomass; and 3) recolonization rates of herbivores relative to higher trophic levels – a possible proxy for productivity. The alternative / null hypothesis is that if trends 1-3 are exhibited by canopy arthropods are independent of plant production. In other words, I expect to find a strong positive correlation between consumer (canopy arthropod) production and plant (aboveground oak tree and local aboveground plant community) production.

Materials and Methods

Aboveground plant production was estimated along two 100 m point-quarter transects and for trees in four live oak groves.

Transects were randomly chosen from a map drawing of all possible 100 m transects along topographic isoclines matched to the surrounding topography of the live oak groves used for this study (figure 1). By chance, the chosen transects ran adjacent or across the groves studied (figure 2). Along each of these transects, ten points at least 5 m apart were randomly selected and at each point, for trees, shrubs, dead wood, and ground cover, taxonomic (species except for herbaceous ground cover) diversity and biomass were calculated. Trees were defined as woody plants with diameter at 30 cm above ground level equal to or exceeding 3 cm. Shrubs were defined as woody plants with diameter at 30 cm above ground less than 3 cm. Dead wood was defined as woody matter touching the ground with diameter at the piece of wood's midpoint greater than 2 cm. Ground cover was expressed in each point-quarter as visual estimate of percentage cover in a 3 m. radius of seedlings of woody plants, grass, and dicot herbs.

Transect points and the trees and shrubs measured were marked with flagging tape to be re-measured after one year to estimate NPP. Four 8 sq. ft. litterfall collection funnels were placed at random locations along each transect (8 total) in late July and the litter they catch will be collected in late December 2012 to estimate the litterfall portion of NPP.

Live oak groves for the study (figure 2) were chosen by exhaustively surveying the entire property for all live oaks greater than 1 ft diameter at breast height (table 1), recording the characteristics of the tree and its surroundings, then selecting two best characteristic-matched (e.g. slope less than 15 degrees, litter and humus layer greater than 6 in. deep, part of closed-canopy forest, at least 3 m. from trails / roads, etc.) groves in both the upland and lowland topographic areas (at least 200 ft from any open standing or flowing water sources for insecticide regulations).

In each live oak grove, live oak tree biomass was calculated, and will be re-measured after one year to estimate productivity. One 8 sq. ft. litterfall collection funnel was placed near the trunk and under the canopy of each tree in all groves (12 total) in late July and the litter will be collected in late December 2012 to estimate the litterfall portion of NPP.

Aboveground arthropod production was estimated by fogging the canopies of live oak trees to calculate the biomass of each morphospecies per unit ground area. Live oak trees were chosen as they are dominant trees in the forest, have canopy morphology amenable to collection by fogging, and have arthropod fauna somewhat representative of other locally dominant trees, with fewer specialists than the three other most dominant tree species in the area (M. Quinn, unpublished data).

Using standardized methods (Adis et al. 1998, Erwin 2012 pers. comm.), trees were fogged with a contact insecticide (1.0% pyrethrin in a nix of highly refined white oil and diesel) from a portable fogger (Golden Eagle Thermal Fogger, Dyna-Fog, USA) held by the author in the understory of the grove, directing fog upwards to evenly cover the entire canopy of the grove, taking about 5-10 minutes, beginning sometime between 0415-0445 hrs, when no breeze was detectable. Collection funnels captured dying insects fallen from pyrethrin-induced spasms for up to 2 hrs after fogging, the appropriate time to capture all affected insects (Adis et al. 1998).

For each fogging, four collection funnels with a 50 sq. ft collection surface area and 20 collection funnels with a 8 sq. ft collection surface area (totaling 360 sq. ft. of under-canopy coverage) were placed directly under the canopy and above the understory of each tree in the grove, covering about 50-90% of the canopy of all the live oaks in the grove. Funnels were secured in place to lines in the canopy the day prior to fogging and were activated (the bottom closed, sometimes with containers attached) and pulled up to position in the two hours before fogging. Individual funnels did not overlap trees, and the tree each funnel covered was recorded on the collected samples so that the tree each arthropod fell from is known.

At three of the four groves (not grove 02 due to time constraints), recolonized arthropods were collected by following the above fogging protocol identically five to six days later, with each collection funnel in almost the exact same location.

All fogging dates and locations are shown in table 2.

Arthopod samples were personally transported by the author for analysis in his adviser's laboratory at the University of California at Berkeley. Once analyzed, samples will be returned to Texas and deposited at the University of Texas Insect Collection, housed in the Lake Austin Centre at Brackenridge Field Laboratory, 3001 Lake Austin Blvd., Austin TX 78703.

Results

Vegetation point-quarter transects suggest the riparian forest has higher plant biomass and woody plant diversity than the hilltop forest (table 3). Productivity comparisons cannot be made until litterfall is collected in late December 2012 transects are re-measured in summer 2013.

Similarly, at the individual tree and grove scales, live oaks have higher biomass in the riparian forests compared to the hilltop forests (table 4). Productivity comparisons cannot be made until litterfall is collected in late December 2012 trees are re-measured in summer 2013.

Of the 12 trees fogged (and 9 trees re-fogged), only the arthropods collected from the initial fog from the first grove (3 trees) have been sorted, identified, and their biomass quantified. Results from this fogging are summarized in table 5.

Discussion / Conclusions

All arthropods collected are expected to be analyzed by May 2013. Preliminary NPP measurements are expected once litterfall samples are collected and analyzed in January 2013. Final NPP measurements are expected once transects and groves are re-measured in summer 2013 and these results analyzed soon after.

The general predicted result at all scales - that animal production directly increases with plant production - will provide more accurate, increased estimates of plant production by including losses to animals. Furthermore, if a close animal-plant production relationship holds within and between trophic guilds, it may be possible to use invertebrate sampling to estimate plant production, even at the resolution of storage compartments such as dead wood, conifer leaves, and litterfall. This invertebrate sampling may give cheaper, quicker, but more accurate estimates of both plant and consumer production in forests. Revealing the nature of producer - consumer production relationships is crucial to understanding basic ecosystem energetics; laws that govern global carbon cycling and storage.

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Tables and Figures

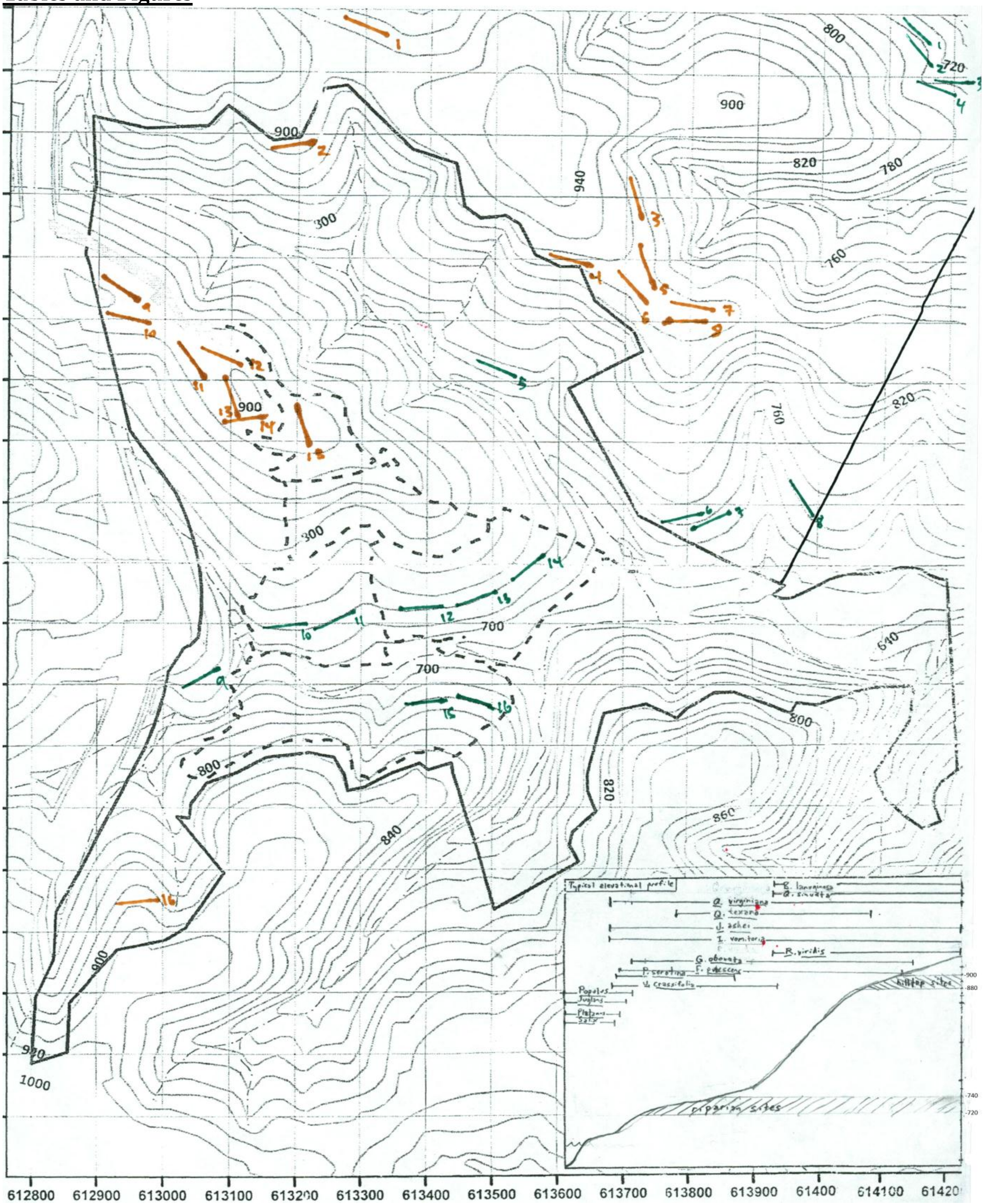

Figure 1. Locations of all potential hilltop (brown) and riparian (green) 100 m transects. Inset: typical topographic profile showing areas of dominance of common trees and shrubs.

	GPS coordinates			GPS coordinates			GPS coordinates		
Tree ID	Latitude	Longitude	Tree ID	Latitude	Longitude	Tree ID	Latitude	Longitude	Tree ID
A	30.3094	97.8252	O	30.3115	97.8249	CA	30.3124	97.8259	XA(2)
B	30.3071	97.8243	P	30.3115	97.8249	DA	30.3124	97.8259	XB
C	30.3075	97.8243	Q	30.3115	97.8249	EA	30.3124	97.8258	XC
D	30.3079	97.8239	R	30.311	97.8257	MA	30.3076	97.8176	XD
E	30.307	97.8243	S	30.311	97.8257	QA	30.3082	97.8177	XE
F	30.3123	97.8256	T	30.311	97.8257	RA	30.3083	97.8176	XF
G	30.3123	97.8256	U	30.311	97.8257	SA	30.308	97.8181	XG
H	30.3123	97.8256	V	30.3105	97.825	TA	30.3071		XH
I	30.3123	97.8256	W	30.3105	97.825	UA	30.3097	97.8188	XI
J	30.3123	97.8256	X	30.3105	97.825	VA	30.3097	97.8188	XM
K	30.3121	97.8252	Y	30.3105	97.825	WA	30.3096	97.8195	XL
L	30.3118	97.8245	Z	30.3102	97.8244	XA	30.3035	97.821	XK
M	30.311	97.8246	AA	30.3116	97.8222	YA	30.3027	97.8211	OA
N	30.311	97.8246	BA	30.3123	97.826	ZA	30.311	97.8216	OB

GPS coordinates			GPS coordinates		fogged tre	GPS coordinates		
Latitude	Longitude	Tree ID	Latitude	Longitude	Tree ID	Latitude	Longitude	Tree ID
30.3074	97.8167	OC	30.3063	97.8241	YA	30.3107	91.8249	97.8249
30.3076	97.8169	OD	30.3057	97.8241	YB	30.3107	91.8249	97.8249
30.3076	97.8169	OE	30.3052	97.824	YC	30.3107	91.825	97.825
30.3077	97.817	OF	30.3052	97.8243	Y2A	30.3112	91.8259	97.8259
30.3077	97.8171	OG	30.3053	97.8243	Y2B	30.3112	91.8257	97.8257
30.3067	97.8179	OH	30.3053	97.8244	Y2C	30.3112	91.8256	97.8256
30.307	97.8177	Y3A	30.3112	97.8259	OA(OF)	30.3052	91.8243	97.8243
30.3069	97.8177	Y3B	30.3112	97.8257	OB(OG)	30.3053	91.8243	97.8243
30.3054	97.8216	Y3C	30.3112	97.8256	OC(OH)	30.3053	91.8244	97.8244
30.3025	97.8192	HwA	30.3056	97.8247				
30.3066	97.8175	HwB	30.3056	97.8247				
30.3066	97.8175	HwC	30.3053	97.8247				
30.3093	97.8252							
30.3072	97.8245							

Table 1. GPS coordinates of all live oak trees >1 ft diameter at breast height found by the author. Note ten trees (FA-PA) were flagged but gps coordinates not taken. Also note in small but live oak-dense pockets in the southwesternmost sector of the property, a number of live oaks were not flagged or their gps coordinates taken. GPS coordinates of the O2 plot are not included.

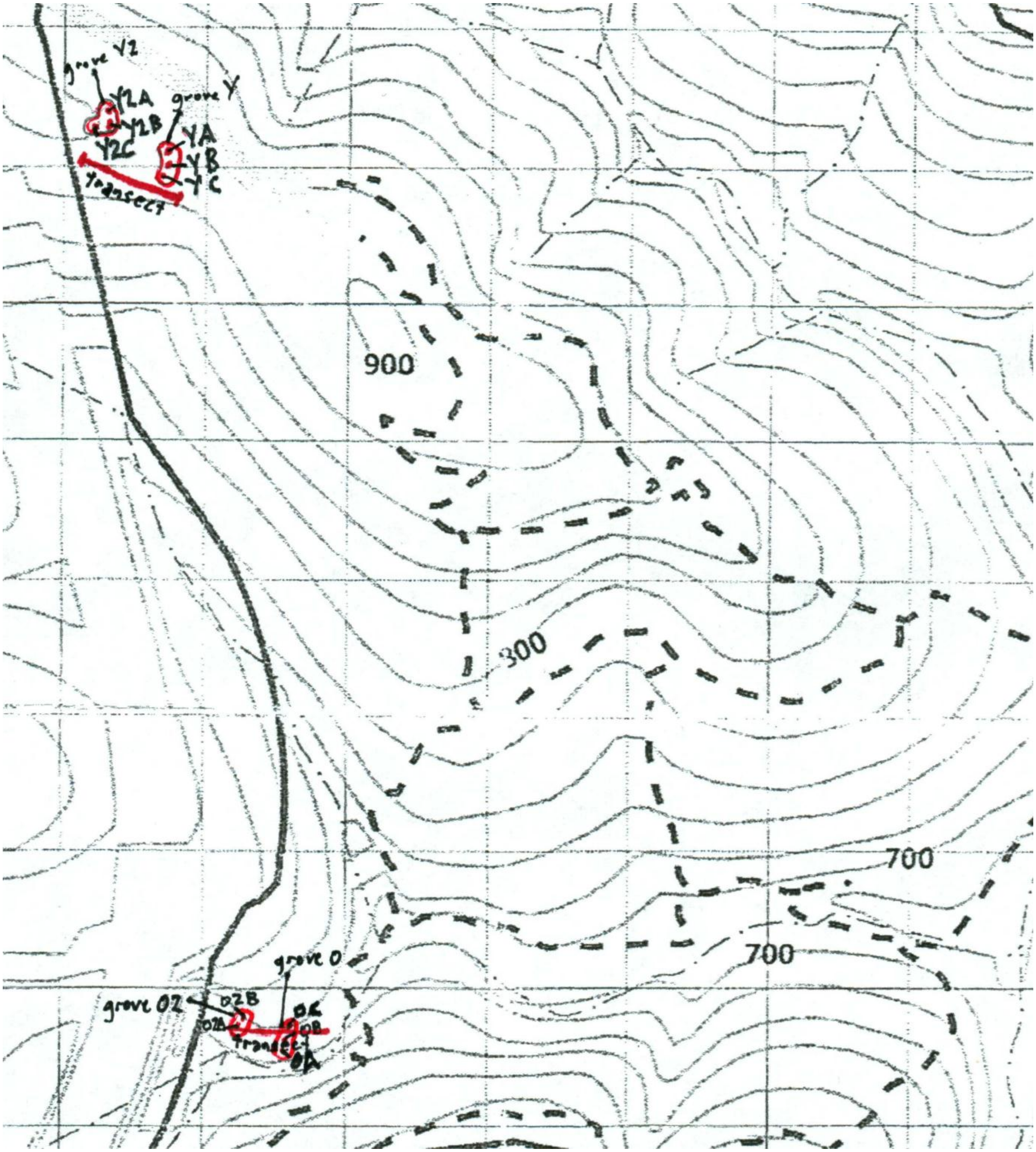

Figure 2. Locations of chosen transects and live oak groves fogged.

Date of fogging	Grove fogged	1st or 2nd fogging of grove
25.VI.2012	Y	1st

31.VI.2012	Y	2nd
03.VII.2012	Y2	1st
09.VII.2012	Y2	2nd
15.VII.2012	O	1st
20.VII.2012	O	2nd
06.VIII.2012	O2	1st
No 2nd fog	O2	2nd

Table 2. Fogging dates and locations.

A) TREES HILLTOP

Species	Absolute den	Relative dens	Total area 30	Total area 13	Mean area 3(	Mean area 13	Relative cove	Relative cove	Relative freq	Importance 3	Importance 1
(all trees)	2294.15	x	104590	94546.84	2892.24	5417.17	x	x	x	x	x
Juniperus ash	1777.97	77.5	62385.9	52340.51	2012.45	1688.4	59.65	55.36	55.56	192.7	188.42
Quercus virgi	229.42	10	37651.7	21472.35	9412.93	5368.09	36	22.71	16.67	62.67	49.38
Quercus texar	x	x	x	x	x	x	x	x	x	x	x
Quercus sinua	57.35	2.5	1644.33	12640.56	1644.33	12640.6	1.57	13.37	5.56	9.63	21.42
Ilex vomitoria	x	x	x	x		x	x	x	x	x	x
Bumelia lanu	57.35	2.5	633.47	7036.52	633.47	7036.52	0.61	7.44	5.56	8.67	15.5
Rhus viridis	172.06	7.5	2274.12	1056.89	758.04	352.3	2.17	1.12	16.67	26.34	25.29
Prunus seroti	x	x	x	x	x	x	x	x	x	x	x

A) TREES RIPARIAN

Species	Absolute den	Relative dens	Total area 30	Total area 13	Mean area 3(	Mean area 13	Relative cove	Relative cove	Relative freq	Importance 3	Importance 1
(all trees)	1010.82	x	121678	96678.21	3084.82	2546.66	x	x	x	x	x
Juniperus ash	758	75	97119.2	76116.75	3237.31	2537.23	79.68	78.59	56.25	210.93	209.84
Quercus virgi	51	5	15024.42	10078.24	7512.21	5039.23	12.44	10.5	12.5	29.94	28
Quercus texar	51	5	8039.56	9083.48	4019.78	4541.74	6.66	9.47	12.5	24.16	26.97
Quercus sinua	x	x	x	x	x	x	x	x	x	x	x
Ilex vomitoria	126	12.5	1049.73	980.63	209.95	196.13	0.86	1.01	12.5	25.86	26.01
Bumelia lanu	x	x	x	x	x	x	x	x	x	x	x
Rhus viridis	x	x	x	x	x	x	x	x	x	x	x
Prunus seroti	25	2.5	444.88	419.1	444.88	419.1	0.36	0.43	6.25	9.11	9.18

B) SHRUBS HILLTOP

Species	Absolute den	Relative dens	Total area 30	Mean area 3(	Relative cove	Relative freq	Importance 3
(all shrubs)	685.83	x	175.22	2.75	x	x	x
Juniperus ash	480.08	70	148	5.29	84.47	50	204.47
Quercus virgi	34.29	5	1.92	0.96	1.1	10	16.1
Quercus texar	x	x	x	x	x	x	x
Ilex vomitoria	68.58	10	3.31	0.83	1.89	10	21.89
Rhus viridis	34.29	5	12.38	6.19	7.06	10	22.06
Garrya obova	34.29	5	7.29	3.64	4.16		19.16
Prunus seroti	x	x	x	x	x	x	x
Foresteria pul	17.15	2.5	0.79	0.79	0.45		7.95
Ulmus crassif	x	x	x	x	x	x	x
Bumelia lanu	17.15	2.5	1.54	1.54	0.88	5	8.38

B) SHRUBS RIPARIAN

Species	Absolute den	Relative dens	Total area 30	Mean area 3(	Relative cove	Relative freq	Importance 3
(all shrubs)	1728.32	x	196.13	5.84	x	x	x
Juniperus ash	259	15	24.83	4.14	12.65	14.29	41.94
Quercus virgi	x	x	x	x	x	x	x
Quercus texar	43	2.5	1.33	1.33	0.67	4.76	7.94
Ilex vomitoria	1037	60	101.04	4.21	51.52	42.86	154.38
Rhus viridis	x	x	x	x	x	x	x
Garrya obova	173	10	28.39	7.1	14.49	14.49	38.78
Prunus seroti	43	2.5	14.93	14.93	7.58	7.58	14.84
Foresteria pul	43	2.5	0.95	0.95	0.48	0.48	7.74
Ulmus crassif	130	7.5	24.65	8.22	12.61	12.61	34.39
Bumelia lanu	x	x	x	x	x	x	x

C) DEAD WO HILLTOP

Species	Absolute den	Relative dens	Total area	Mean area	Relative cove	Relative freq	Importance
(all dead woc	87.33	x	477.97	13.17	x	x	x
Juniperus ash	10162	77.5	352.36	11.37	73.72	58.82	210.04
Quercus virgi	1311.2	10	54.83	13.71	11.47	17.65	39.12
Quercus texar	x	x	x	x	x	x	x
Quercus sinua	655.61	5	34.88	17.44	7.3	5.88	18.8
Rhus viridis	655.61	5	25.15	12.57	5.26	11.76	22.03
Ilex vomitoria	327.8	2.5	10.75	10.75	2.25	5.88	10.63

C) DEAD WO(RIPARIAN

Species	**Absolute den**	**Relative dens**	**Total area**	**Mean area**	**Relative cove**	**Relative freq**	**Importance**
(all dead woo	143.95	x	547.76	14.05	x	x	x
Juniperus ash	1448	30	237.61	19.8	43.38	40	83.38
Quercus virgi	2051	42.5	182.41	10.73	33.3	35	68.3
Quercus texar	1327	27.5	127.7	11.61	23.32	23	48.32
Quercus sinu	x	x	x	x	x	x	x
Rhus viridis	x	x	x	x	x	x	x
Ilex vomitoria	x	x	x	x	x	x	x

D) GROUNDC	**HILLTOP**	**RIPARIAN**
Type	**Mean percen**	**Mean percen**
(all groundco	36.5	21.7
Grass	23.6	8.78
Seedlings	7.03	10.2
Dicot herbs	5.88	2.73

Table 3. Summarized point-quarter transect results for trees (a), shrubs (b), dead wood (c), and ground cover (d). Note data do not yet incorporate height of trees and shrubs nor length of dead wood pieces. Units: Absolute density in individuals/ha, relative density as percent, total and mean area in sq. cm., relative cover and frequency as percent, and importance (no units) can range from 0-300. Note also the tree tables show values calculated for both circumference at 30 cm and 130 cm above the ground, the shrub tables show values calculated for diameter at 30 cm, and the dead wood tables show values calculated for diameter at the center of the piece of wood.

Oak Biomass data

plot	oak	circ.30			circ.130				height
Y	A	120	295		82	168	157	398.78	737
	B	401			208	184			747
	C	218			174				724
Y2	A	223			212				826
	B	212			183				823
	C	220			201				754
O	A	249			209				756
	B	666			171	328	293		863
	C	132	195	178	126	160			706
O2	A	165	143		134	169			800
	B	330	353		270	402			800

Table 4. Location and size of live oaks fogged. All numbers in centimeters.

A)

Order	# individuals	Families	Species
Acari	6	1	4
Araneae	129	3	20
Blatteria	4	1	2
Coleoptera	18	7	12
Collembola	25	3	6
Diptera	45	4	12
Hemiptera	279	8	23
Hymenoptera	234	11	21
Isopoda	6	1	1
Isoptera	374	1	1
Lepidoptera	6	4	4
Neuroptera	15	3	3
Opiliones	1	1	1
Orthoptera	3	1	2
Psocoptera	735	1	3
Thysanoptera	6	1	2
Thysanura	394	1	1
Totals	2280	52	118

B)

Tree	Coverage (	# individu	#/sq.ft.	Vol. (mL)	mL./sq.ft.
A	106	1064	10.04	10.6	0.1
B	198	967	4.88	4.4	0.02
C	56	931	16.63	0.9	0.02

Table 5. Summarized results of arthropods collected by first fogging of hilltop live oak grove listing (A) minimum taxonomic diversity for orders, families, and (morpho-)species, and (B) biomass data, showing area covered by collection funnels per tree, total number and volume (estimated as the product of each specimen's length, width, and height) of arthropods collected per tree, and such number and volume divided by area covered by collection funnels.

NOTE: The raw data spreadsheet is included with this report by email attachment.