Evolution meets ecology: Can native grasses evolve in response to cheatgrass invasion?

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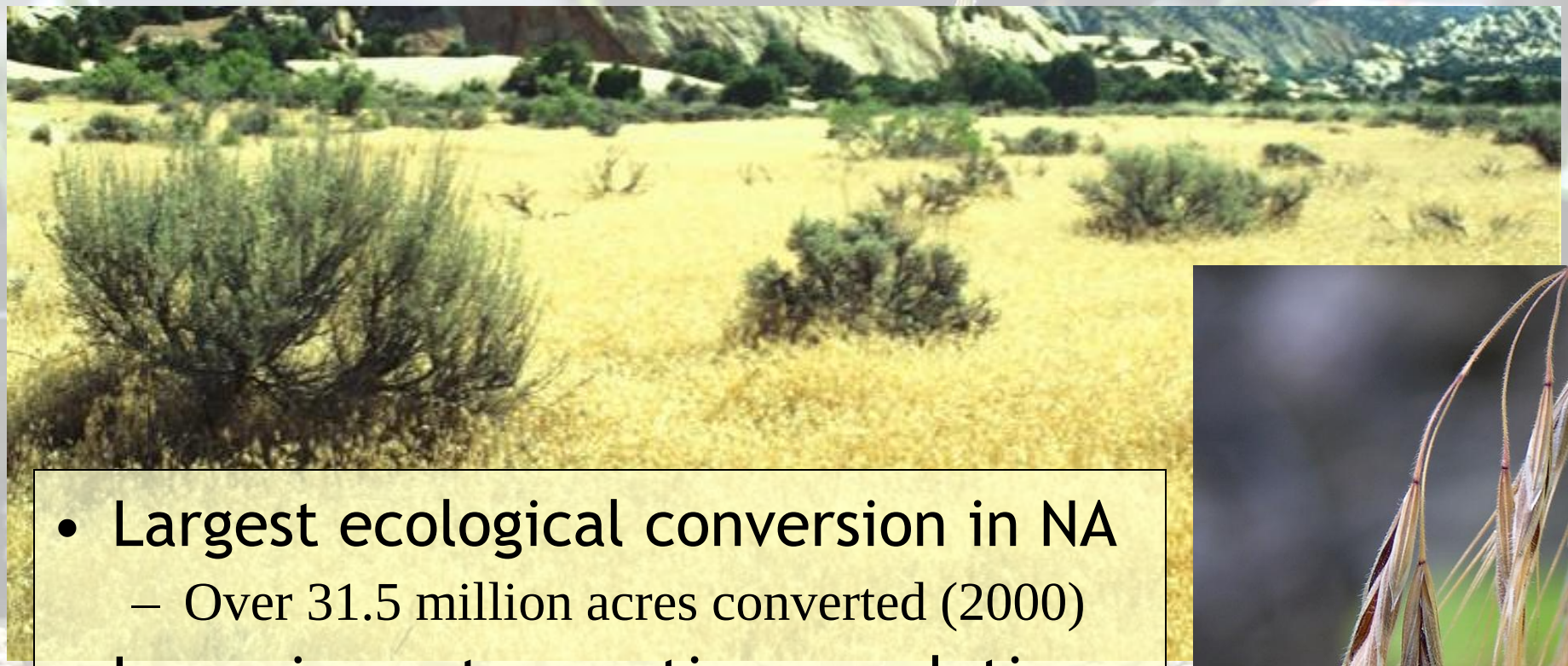
Cheatgrass is changing the Great Basin (maybe irreversibly)



- Largest ecological conversion in NA
  - Over 31.5 million acres converted (2000)
- Large impact on native populations
  - More frequent fires, altered soil conditions
  - Changing succession pathways
- Long-term alteration
  - >100 years in some areas

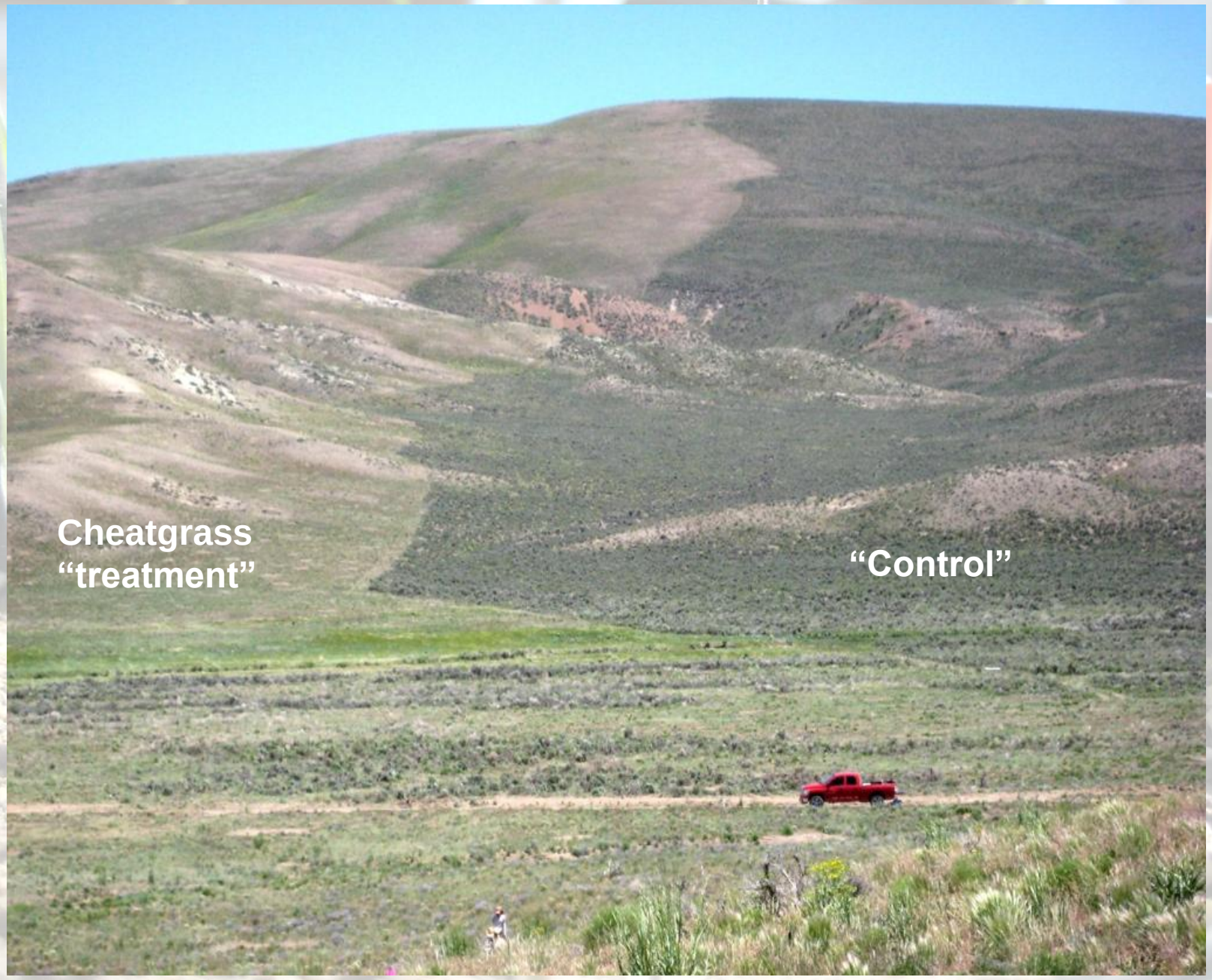
Big idea slide: are these plants special?

Why care about potentially rapid-evolving natives?

- Bodes well for persistence of natives in irreversibly invaded systems

- May improve revegetation of invaded areas
  - Consider collecting from long-invaded populations or those that exhibit greater competitive ability

Studying invasion along boundaries



Can native grasses evolve in response to cheatgrass invasion?

Evaluating potentially adaptive traits— 2 approaches

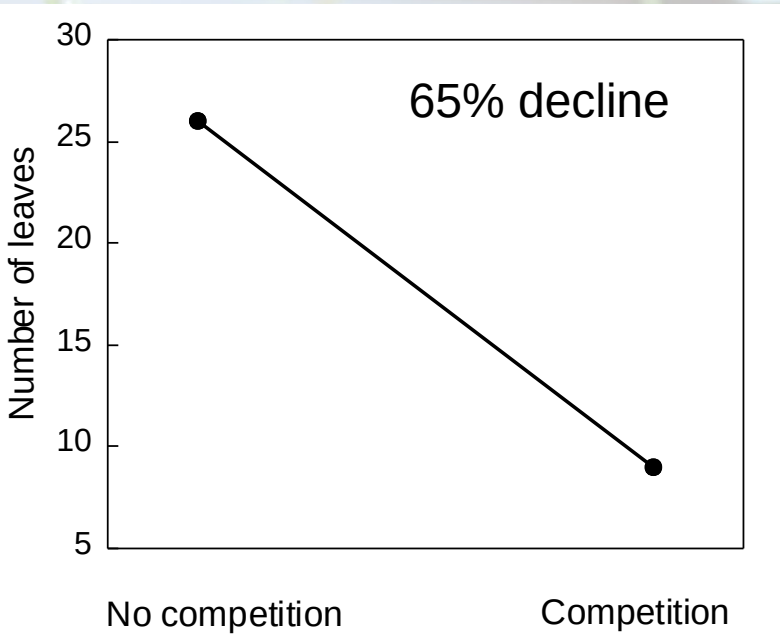
- Liberal / Exploratory
  - Under competition, which traits differ between invaded & uninvaded plants? (drift)
  - Are plants from invaded areas more competitive?
- Conservative / Confirmatory
  - What traits improve competitive ability in uninvaded plants?
  - Do these traits display genetic variation?
  - Have they shifted in invaded conspecifics?

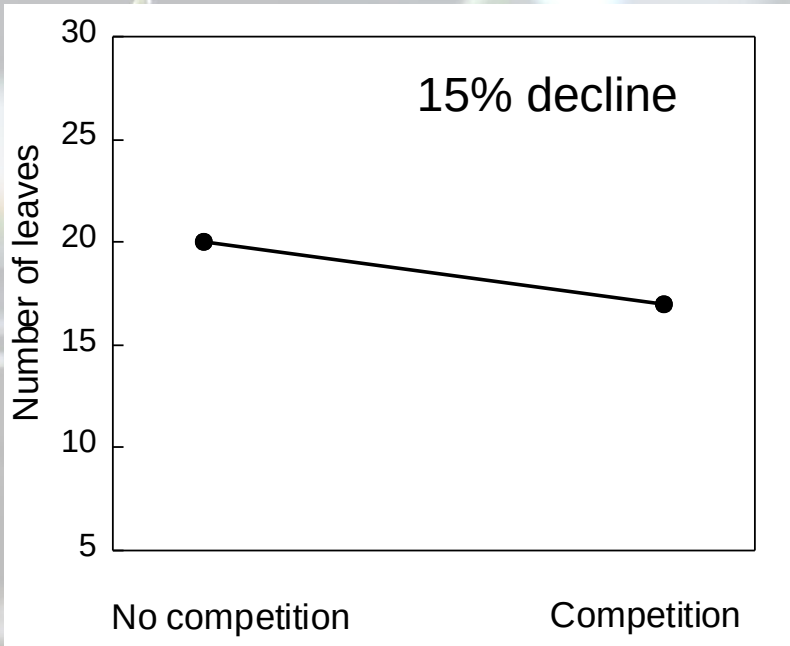
Are seedlings from invaded areas more competitive?

- Common garden greenhouse experiment
  - Invasion status—Invaded or uninvaded
  - Family—25 invaded & 25 uninvaded; siblings = seeds from a single plant
  - 2 growing conditions—cheatgrass (left photo) & no cheatgrass (right photo)

- End-of-season destructive harvesting
- Competitive ability measures
  - –Cheatgrass biomass
  - –Competitive performance index

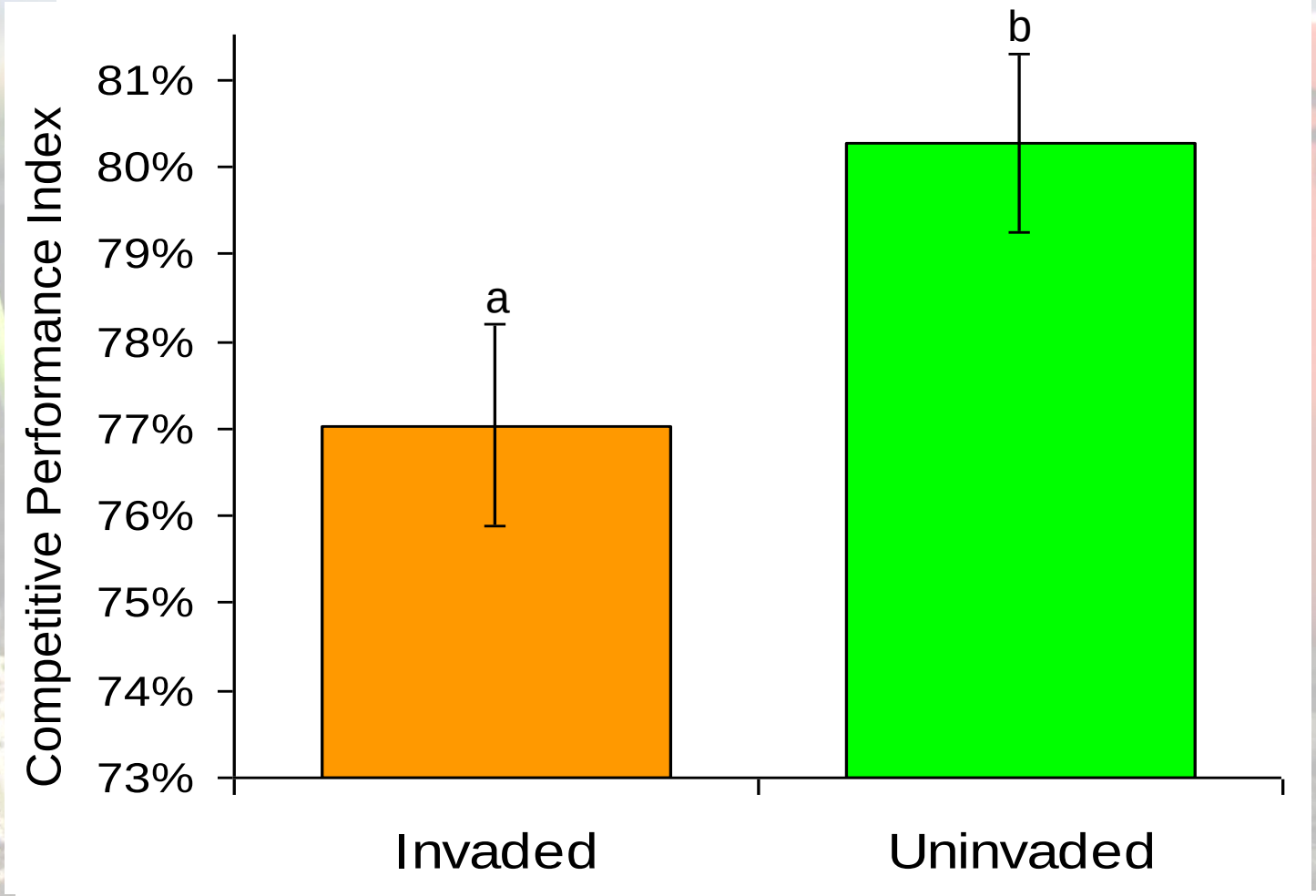
Competitive performance index





- Relative % decline in biomass
- Lower CPI ≈ greater tolerance of competition

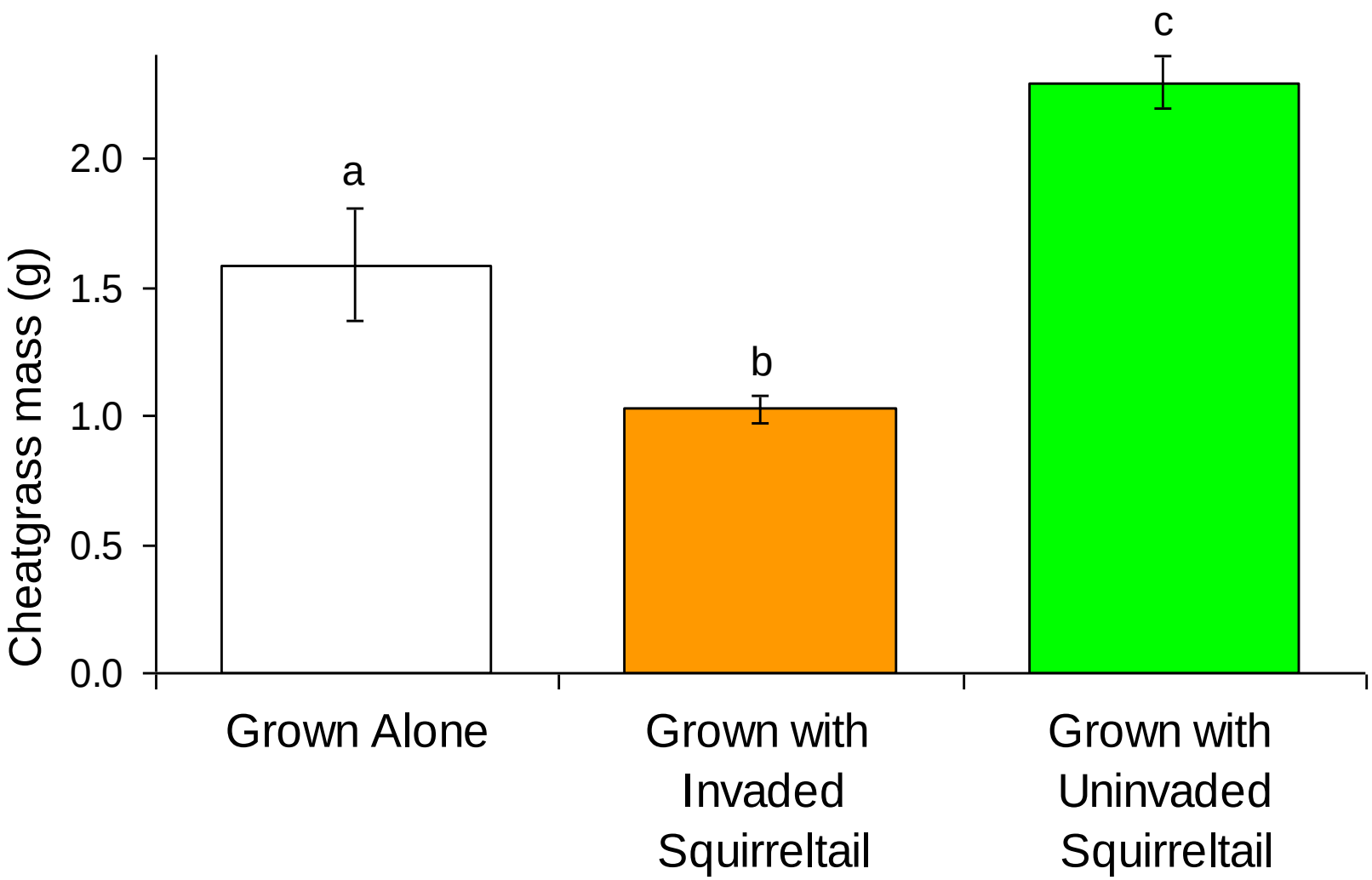
Invaded plants are better tolerators of competition



$F_{1,50}$=6.30, r^2=0.31, P<0.0001

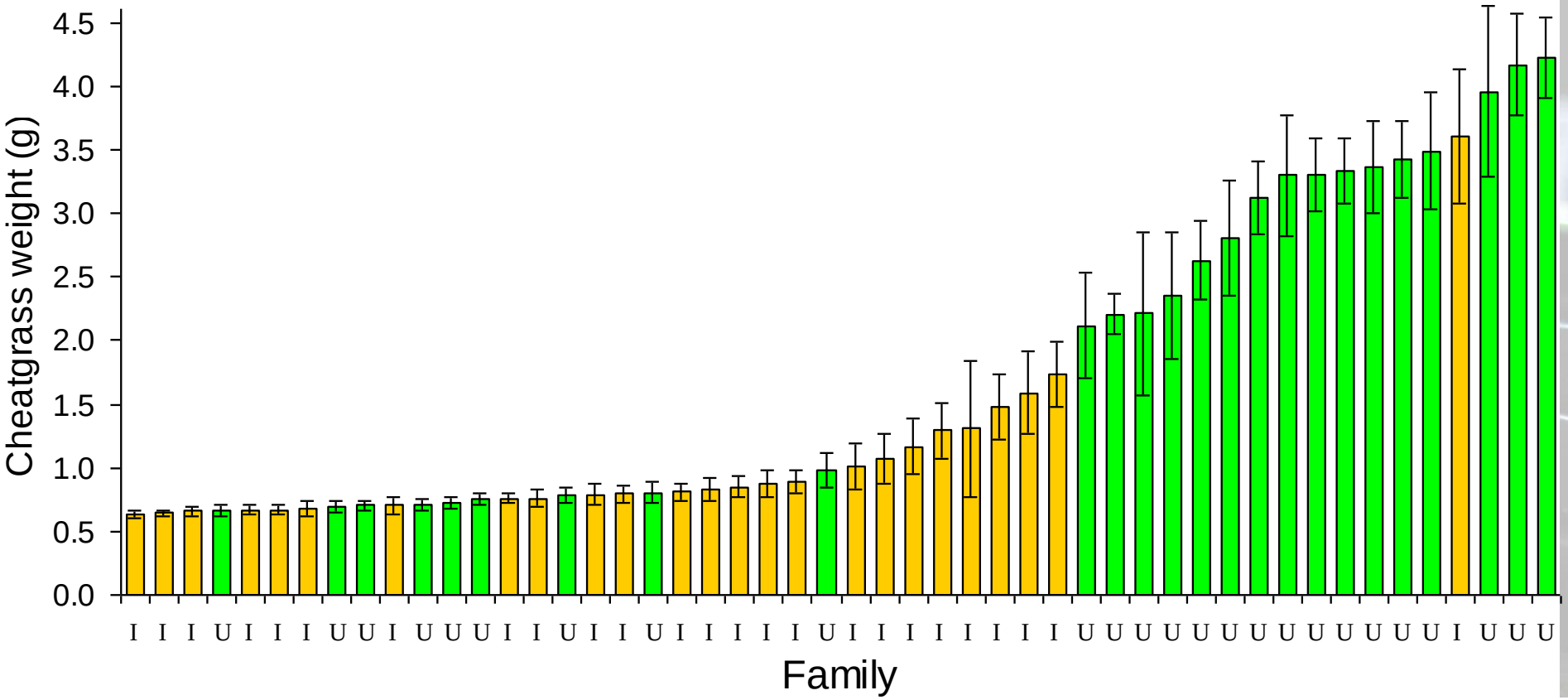
Eight of top ten most competition tolerant families are invaded

Invaded plants suppress cheatgrass biomass



$F_{2,508}$=60.55, r^2=0.19, P<0.0001

Families vary in cheatgrass suppression



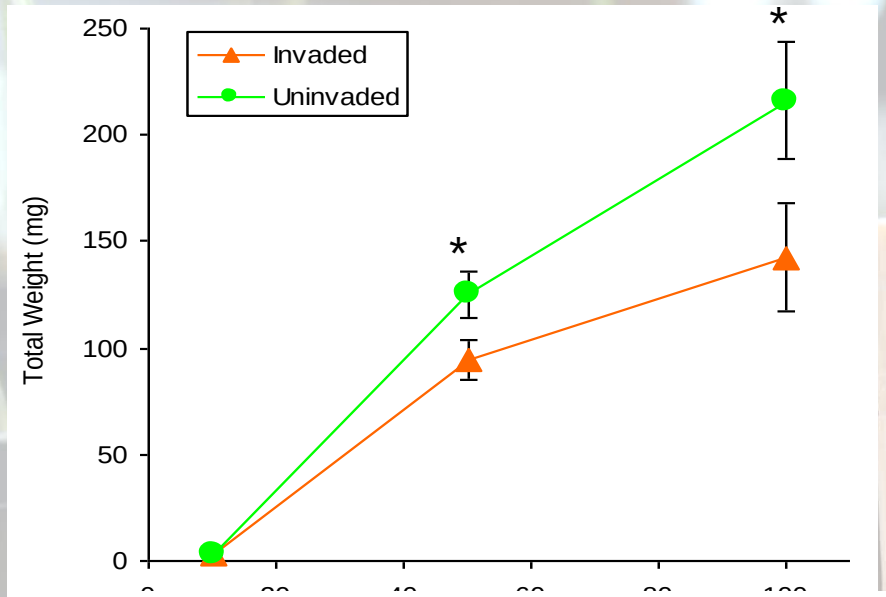
$F_{42,476}$=5.73, r^2=0.68,P<0.0001

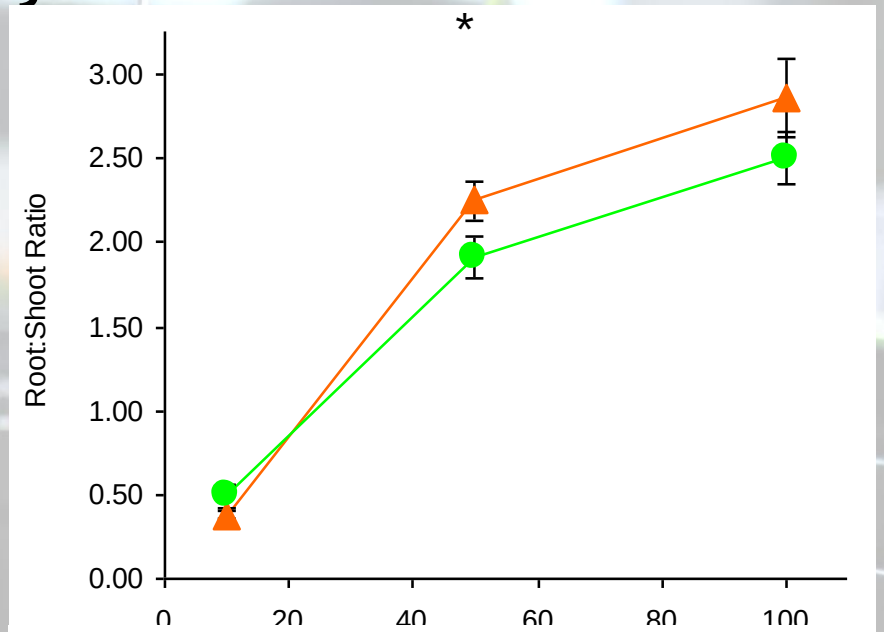
- There is significant genetic variation in the ability to suppress cheatgrass within a single population
- Which seed would you use in cheatgrass invaded areas?

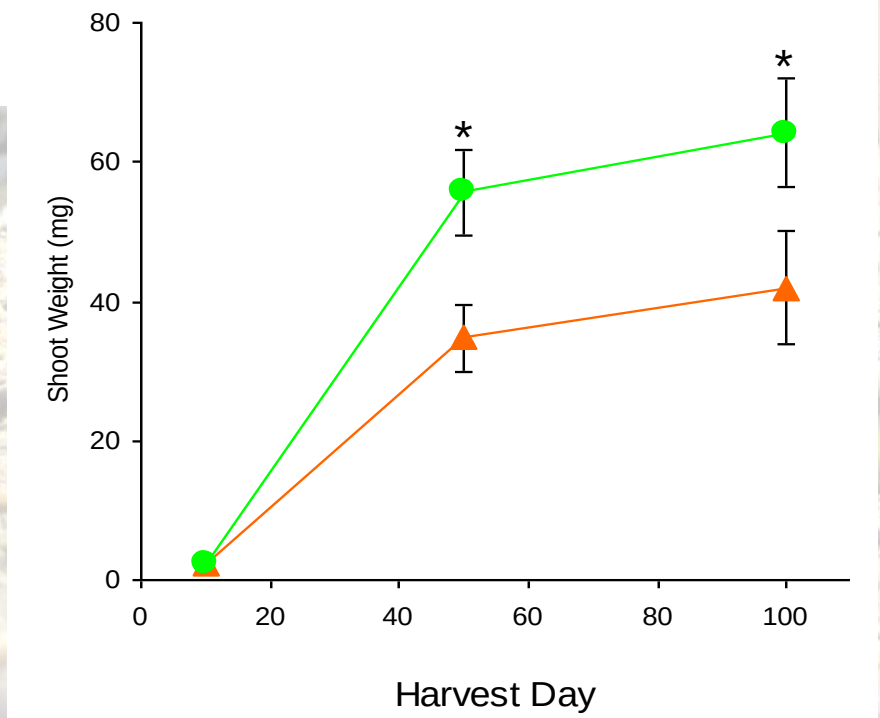
Under competition, do traits vary by invasion status?

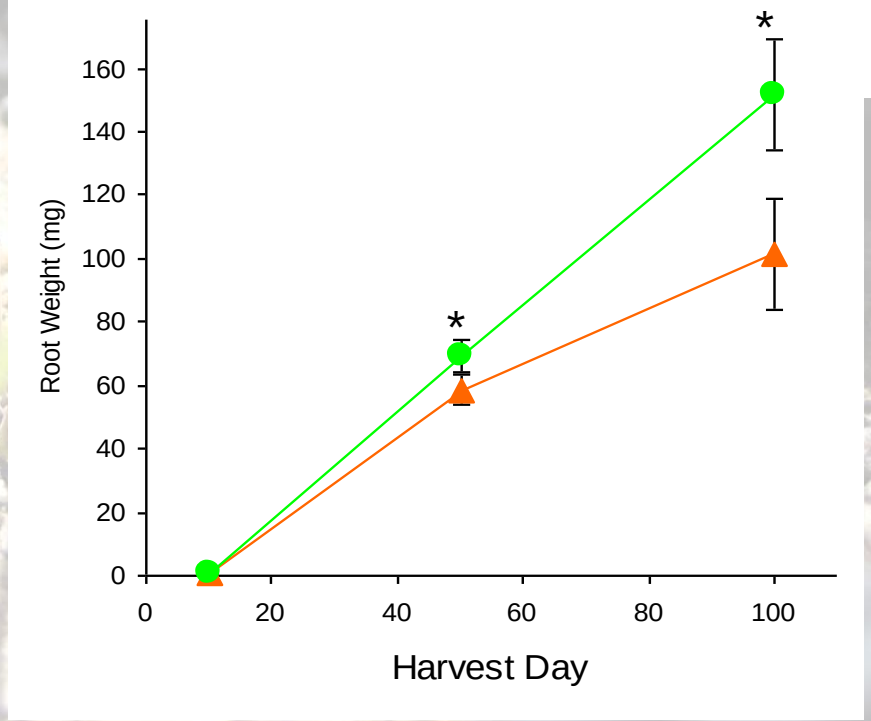
- Measure 47 growth traits in competition
  - –6+ siblings from each family grown with cheatgrass
  - –3 Sequential destructive harvests—10, 50, & 100 days
  - –15 traits varied by invasion status

Biomass traits vary by invasion status

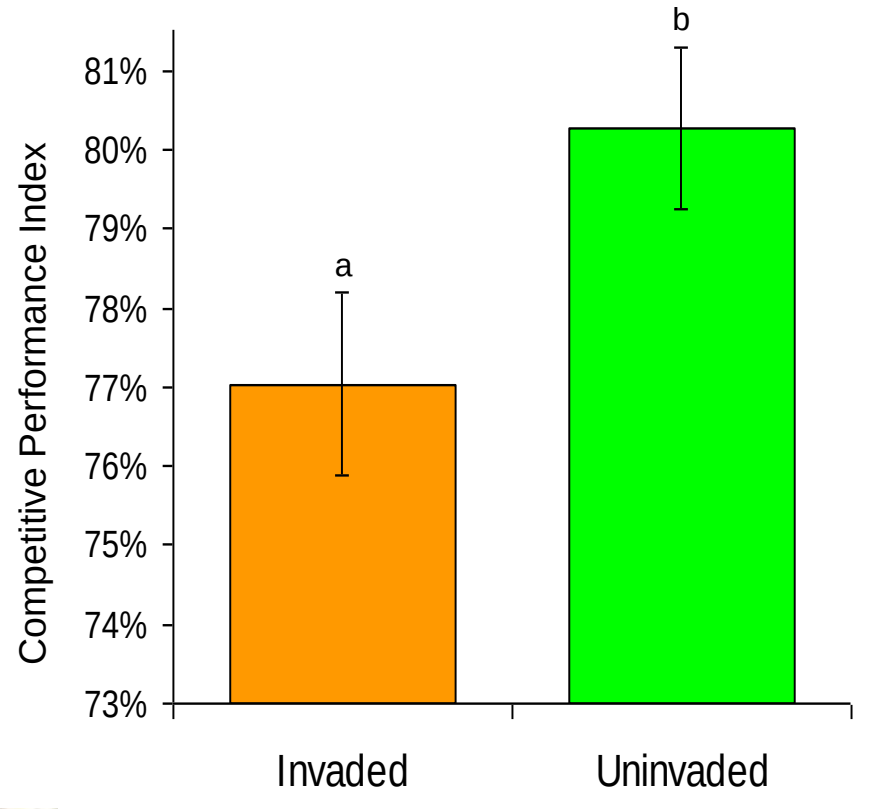


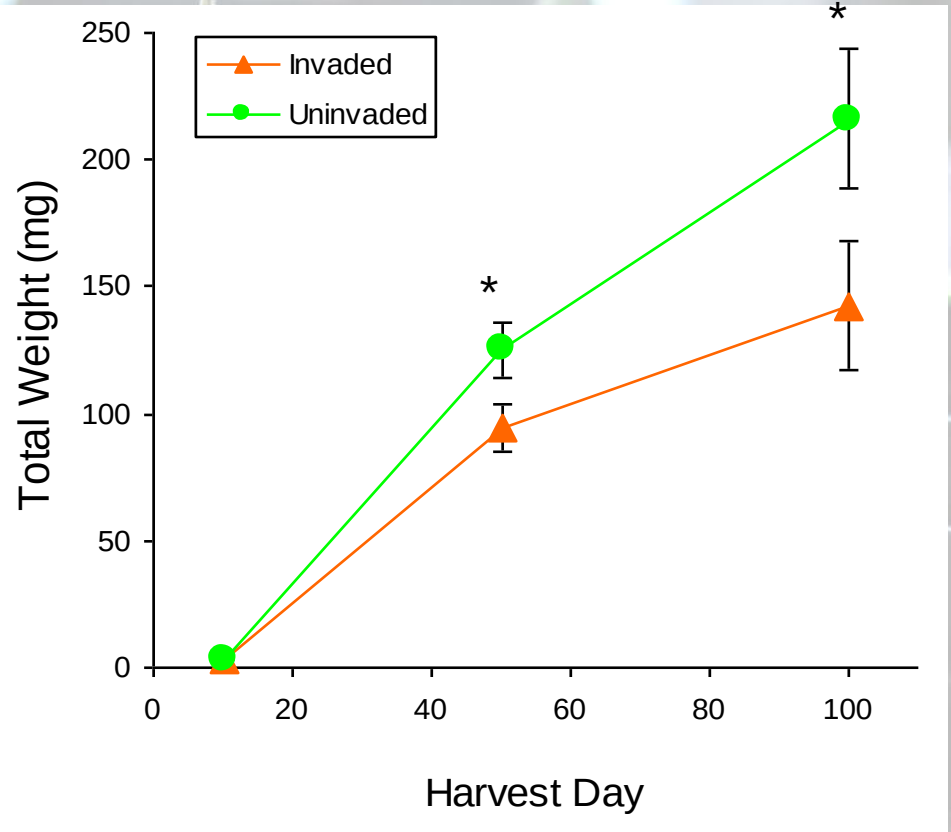






Isn't bigger supposed to be better?



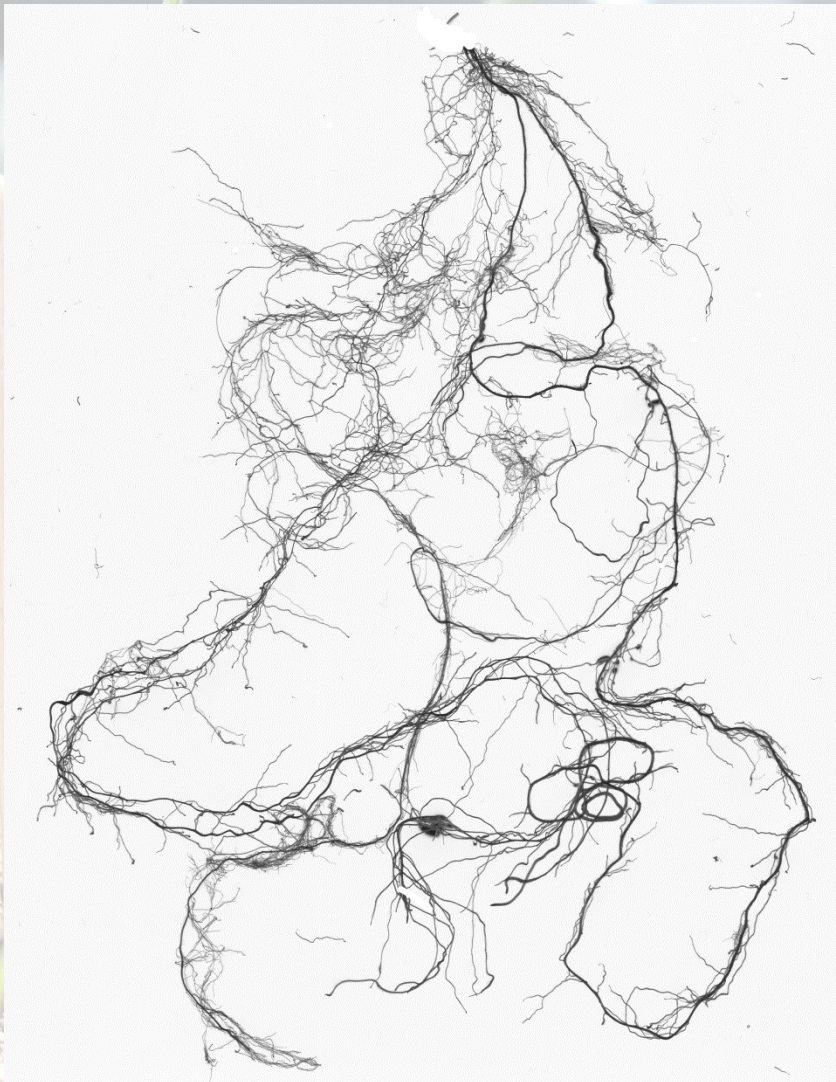


Decoupling of biomass and competitive ability

We have seen this in a number of experiments: Kulpa & Leger in review; Rowe & Leger 2011; Leger 2008; Leger unpublished data (annual forbs *Collinsia, Cyptantha)*

Root diameter traits vary by invasion status

- Plants from invaded areas
  - More fine roots (<0.2mm) & fewer large roots (>0.4mm)
  - Higher fine root percentage
- Linked to resource capture & competitive ability in Great Basin
  - e.g. Bilbrough & Caldwell 1997, James et al. 2009



Example of an invaded status plant‘s root system at 50 days

Approaches to evaluating adaptive traits

- Liberal / Exploratory
  - Under competition, which traits differ between invaded & uninvaded plants?
  - Are plants from invaded areas more competitive?
- Conservative / Confirmatory
  - What traits improve competitive ability in uninvaded plants?
  - Do these traits display genetic variation?
  - Have they shifted in invaded conspecifics?

Looking at trait shift across invasion status

1. Correlated with CPI in uninvaded plants alone ≈ role in competitive ability
   - 3 of 47 measured traits
   - All early root growth characteristics
   - More root forks ≈ highly branching root system

Trait	Correlation with competitive ability		Family level variation	
	P	r^2	P	r^2
10 day R:S	**0.0178**	0.14	0.6934	0.42
10 day fine root length (0.1-0.2mm)	**0.0309**	0.35	0.4279	0.53
10 day root forks	**0.0427**	0.15	**0.0224**	0.70

2. Family level differences ≈ genetic variation
   - 10 day root forks
3. Varies by invasion status ≈ trait shift
   - None

Conclusions

- Native grasses may be adapting in response to cheatgrass
  - Invaded plants are better cheatgrass tolerators & suppressors
- Early root growth probably plays a role in competitive ability
  - Best competitors have more fine root length, higher root:shoot ratio, & more root forks
- Certain traits exhibit genetic variation
  - But shift across invasion status couldn’t be verified

How might this affect management decisions?

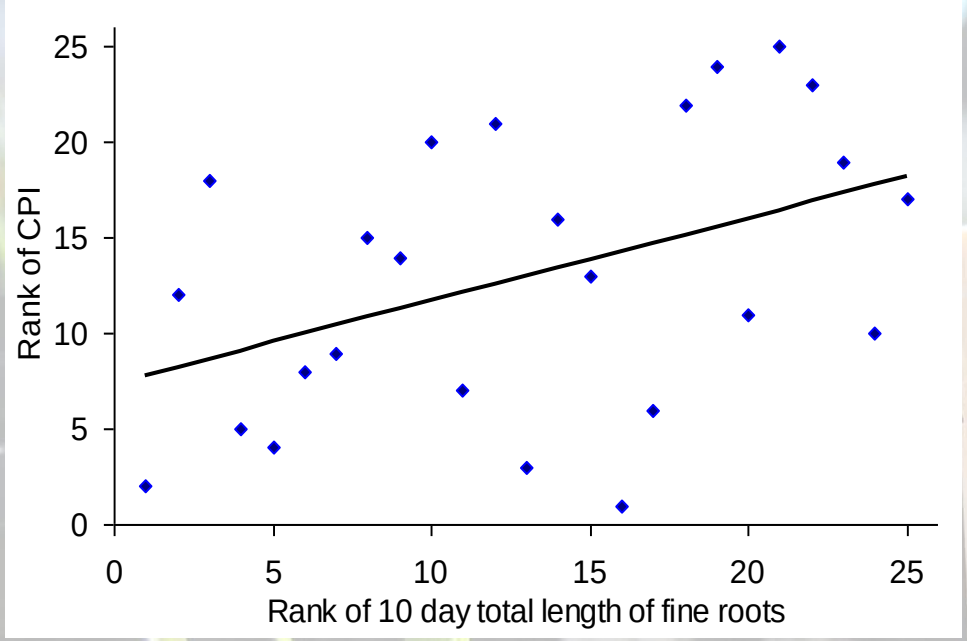
- Reexamine management of invaded sites
  - Don't give up on ~~ugly~~ scrappy native grass populations; their evolutionary history may be important
  - Question the use of non-local seed near long-invaded sites
- Reexamine seed material choices
  - Consider collecting from long-invaded populations or those that exhibit greater competitive ability
- Embrace 'evolutionarily enlightened management'

Ashley et al. 2003

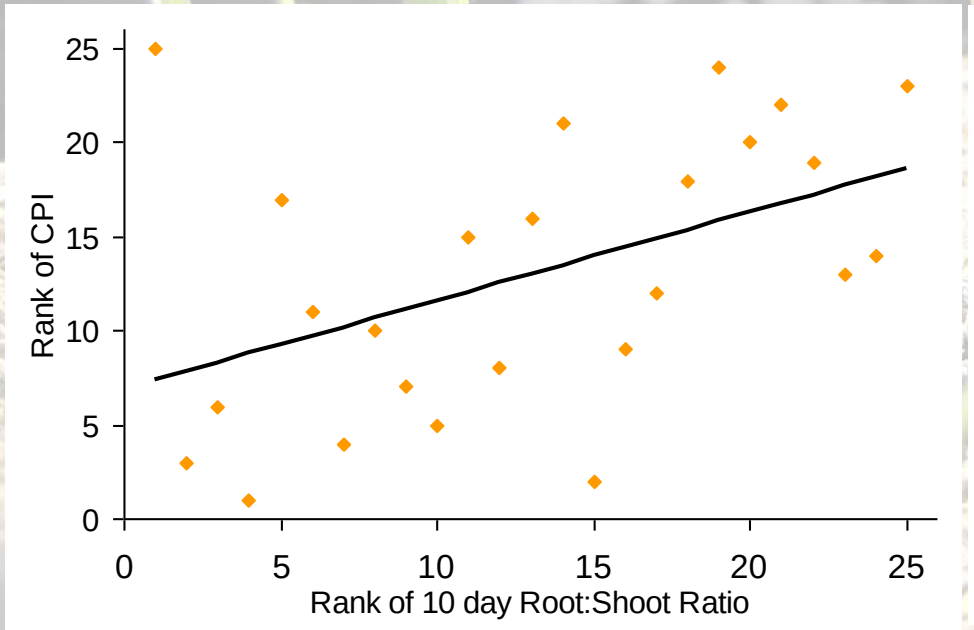
Acknowledgements

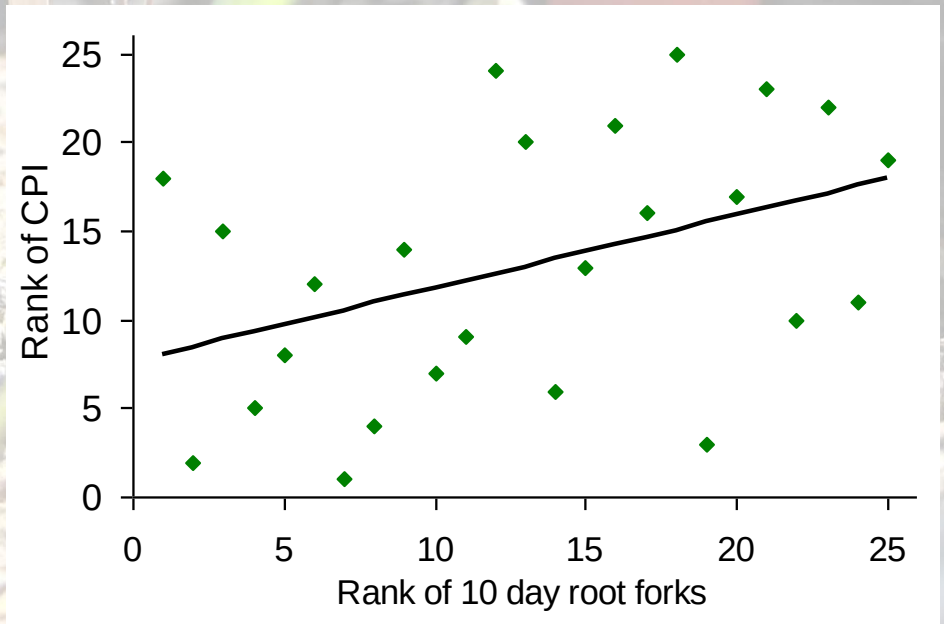
- Field & Lab Support
  - Sandra Li
  - Erin Goergen & Erin Espeland
  - Akiko Endo, Anna Koster, Bryce Nance, Phil Samuels, Kestrel Schmidt, Cassandra Woodward, & Hiroaki Zamma
- California Department of Fish & Game

Early root traits plays a role in competitive ability



- Most competitive CPI is ranked #1 & correlates with:
  - More fine root length
  - Higher root:shoot ratio
  - More root forks
- Common adaptations for nutrient poor conditions



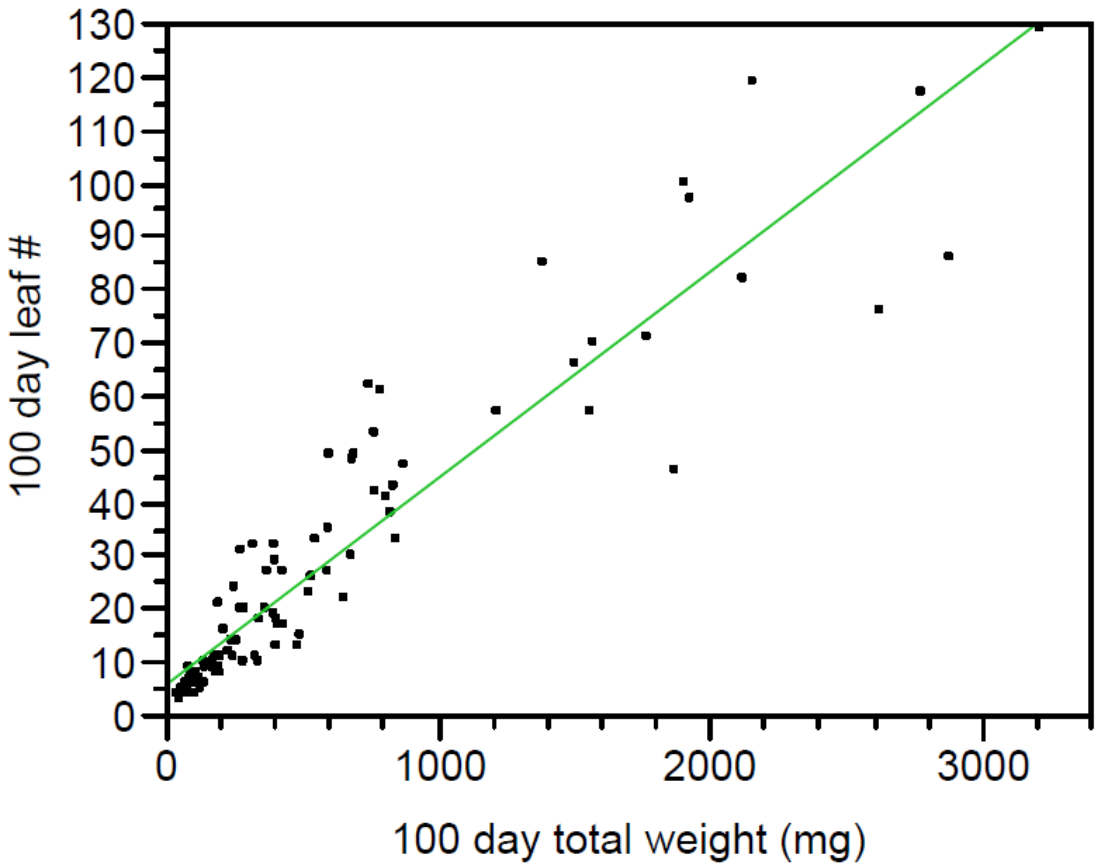


Seed mass effects

	F-ratio	n	df	P	r^2	Uninvaded mean mass (mg)	Invaded mean mass (mg)
Seed mass	69.77	991	1	<0.001	0.44	4.78±0.039	4.32±0.046
Next generation seed mass	209.72	200	1	<0.001	0.91	6.1±0.04	5.2±0.04

- Growth traits that vary by seed mass
  - Total, root, & shoot biomass at 10 days
  - 3 largest root diameter classes at 10 days
- No correlation with seed mass
  - CPI
  - Cheatgrass biomass
  - Any 50 or 100 day growth traits
- Genetic variation in next generation seed mass

Selection of Leaf # for CPI



$P<0.0001$, $F_{1,100}=672.98$, $r^2=0.87$

Root biomass ($P<0.0001$, $F_{1,100}=223.42$, $r^2=0.70$)

Shoot biomass ($P<0.0001$, $F_{1,101}=10005.48$, $r^2=0.91$)

- Strongly correlated to biomass
- Easier to collect
- Greater sample size
  - n=100 for biomass measures
  - n=669 for leaf #
- Higher power for analysis
  - Invasion status
    - Competition Power =1.000
    - Control Power =1.000
  - Family
    - Competition Power =1.000
    - Control Power =0.9987

Growth traits that vary by invasion status or family

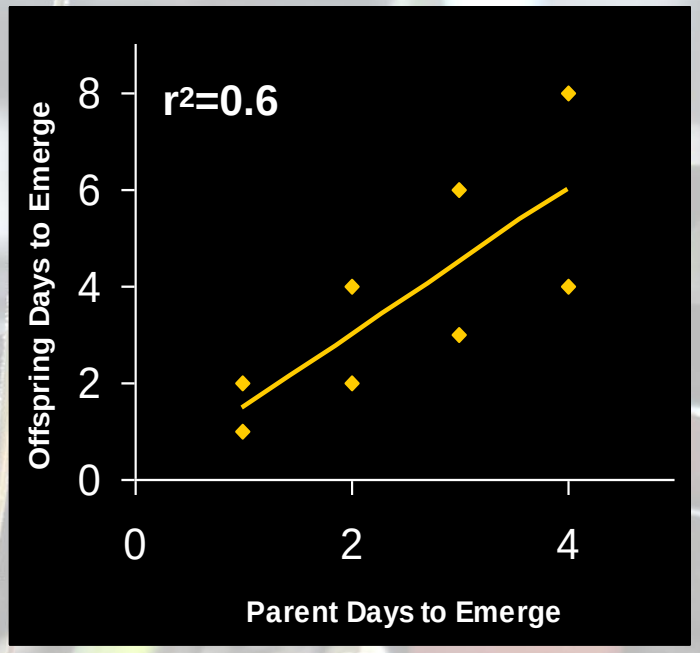
Response Variable	n	r^2	Status			Site			Family		
			F	df	P	F	df	P	F	df	P
Seed mass (g)	991	0.44	69.77	1	**<0.0001**	7.72	6	**<0.0001**	14.14	42	**<0.0001**
Emergence Date	950	0.09	0.08	1	0.7799	1.98	6	0.0664	1.86	42	**0.0009**
Early growth rate (leaf #)	402	0.47	33.93	1	**<0.0001**	23.17	6	**<0.0001**	3.04	42	**<0.0001**
Early growth rate (leaf length)	402	0.29	11.91	1	**0.0006**	10.58	6	**<0.0001**	1.69	42	**0.0065**
10 day total mass (mg)	99	0.62	0.01	1	0.9324	2.38	6	**0.0425**	1.58	42	0.0610
10 day (0.201-0.300mm)	99	0.69	0.89	1	0.3495	6.33	6	**<0.0001**	1.72	42	**0.0346**
50 day total mass (mg)	147	0.61	7.09	1	**0.0091**	10.35	6	**<0.0001**	1.97	42	**0.0033**
50 day shoot mass (mg)	148	0.66	10.64	1	**0.0015**	12.31	6	**<0.0001**	2.40	42	**0.0002**
50 day root mass (mg)	148	0.57	0.76	1	0.3840	10.04	6	**<0.0001**	1.73	42	**0.0138**
50 day R:S	147	0.5	6.40	1	**0.0130**	5.74	6	**<0.0001**	1.39	42	0.0953
50 day leaf #	148	0.66	8.42	1	**0.0046**	12.45	6	**<0.0001**	2.48	42	**0.0001**
50 day root total root length (cm)	145	0.53	0.11	1	0.7349	4.21	6	**0.0008**	2.02	42	**0.0026**
50 day root tips	145	0.5	2.69	1	0.1041	3.76	6	**0.0021**	1.69	42	**0.0185**
50 day root forks	145	0.56	1.50	1	0.2230	3.69	6	**0.0024**	2.35	42	**0.0003**
50 day root diameter (mm)	145	0.64	58.21	1	**<0.0001**	4.39	6	**0.0006**	1.55	42	**0.0412**
50 day % fine roots (≤0.200mm)	145	0.65	40.05	1	**<0.0001**	6.46	6	**<0.0001**	1.83	42	**0.0079**
50 day (0.000-0.100mm)	145	0.57	0.12	1	0.7291	3.32	6	**0.0051**	2.50	42	**0.0001**
50 day (0.101-0.200mm)	145	0.49	3.91	1	0.0509	2.82	6	**0.0144**	1.70	42	**0.0169**
50 day (0.301-0.400mm)	145	0.53	3.67	1	0.0584	6.15	6	**<0.0001**	1.55	42	**0.0398**
50 day (>0.400mm)	145	0.64	37.90	1	**<0.0001**	5.38	6	**<0.0001**	2.02	42	**0.0026**
100 day total mass (mg)	49	0.46	7.45	1	**0.0093**	4.80	6	**0.0009**	--	--	--
100 day shoot mass (mg)	50	0.42	7.22	1	**0.0103**	4.11	6	**0.0025**	--	--	--
100 day root mass (mg)	49	0.44	6.39	1	**0.0154**	4.40	6	**0.0016**	--	--	--
100 day leaf #	482	0.57	66.34	1	**<0.0001**	39.66	6	**<0.0001**	6.17	42	**<0.0001**

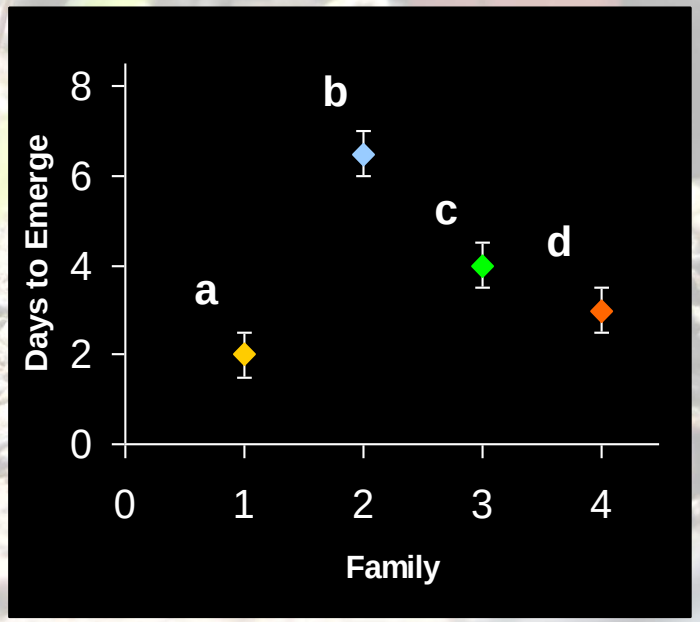
Growth Traits in Competition

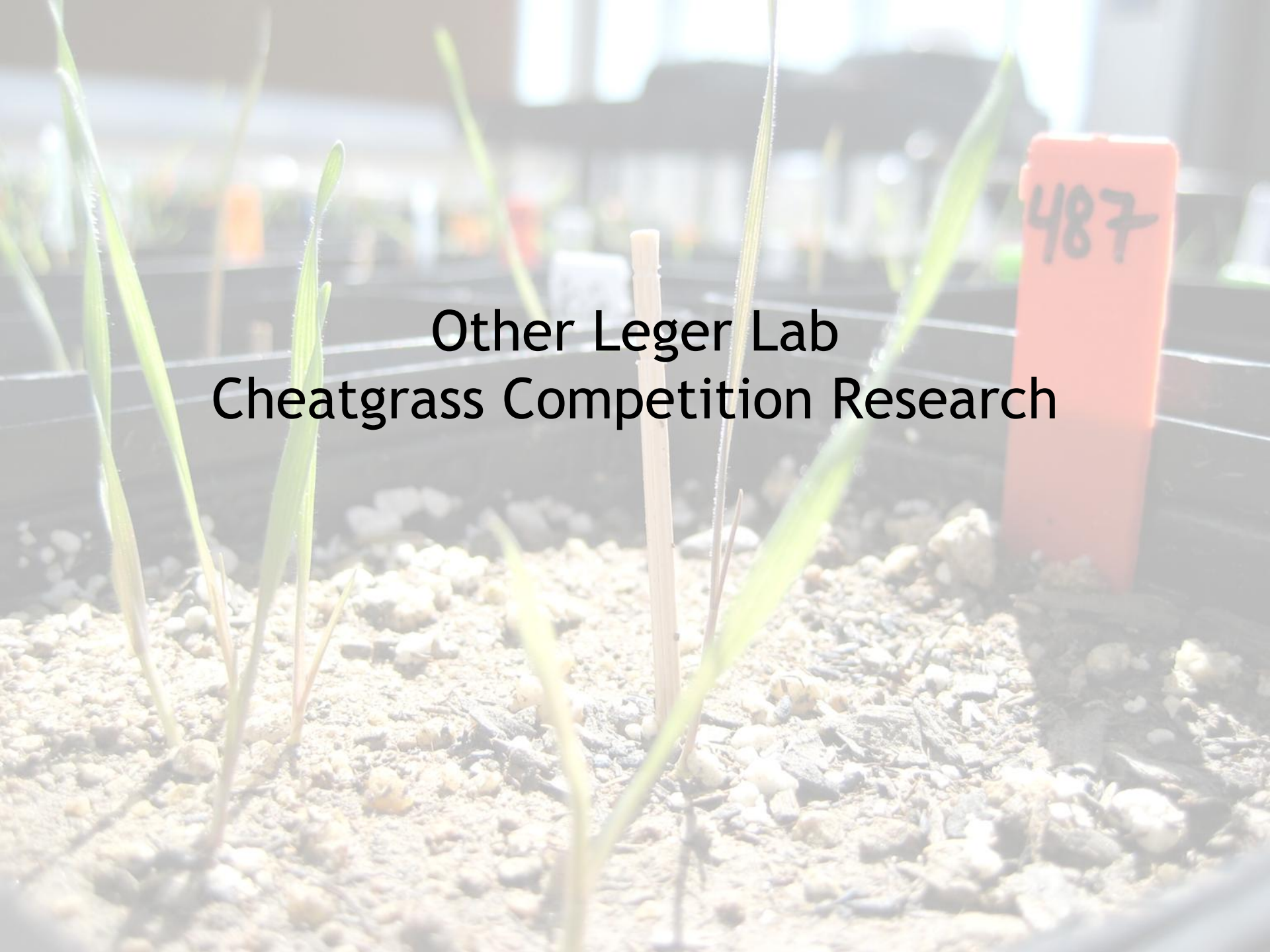
	10 day				50 day				100 day			
	Uninvaded		Invaded		Uninvaded		Invaded		Uninvaded		Invaded	
Total mass (mg)	3.10	0.11	3.02	0.11	125.03	11.32	93.94	9.30	215.98	27.56	142.38	25.57
Shoot mass (mg)	2.17	0.08	2.20	0.07	55.67	6.13	34.82	4.83	64.18	7.81	41.89	8.11
Root mass (mg)	0.93	0.06	0.82	0.05	69.36	5.66	58.55	4.94	151.80	20.47	101.23	17.50
R:S	0.49	0.07	0.38	0.02	1.91	0.13	2.25	0.12	2.51	0.15	2.86	0.24
Leaf number	1.22	0.06	1.20	0.06	8.04	0.60	6.32	0.46	10.84	0.36	7.81	0.27
Root Length (cm)	17.12	0.97	16.80	0.87	671.18	44.97	684.00	43.54	1067.57	107.53	1160.37	154.00
Root Tips	49.92	5.12	48.80	3.88	1535.03	130.21	1389.32	120.84	4026.08	467.44	3717.69	538.23
Root Forks	49.22	3.78	51.88	4.87	3361.81	364.69	3926.24	365.90	7143.76	1022.56	8096.50	1537.62
Root Diameter (mm)	0.32	0.01	0.31	0.01	0.26	0.01	0.21	0.00	0.23	0.01	0.21	0.01
Fine root percentage (<0.200mm)	33.58%	1.67%	38.77%	1.55%	72.05%	0.72%	77.96%	0.63%	74.30%	1.37%	78.08%	1.06%
Root Diameter Size Classes (root length in cm)												
0.000-0.100mm	1.86	0.22	1.68	0.15	216.22	20.91	237.86	21.85	423.41	49.67	451.23	66.27
0.101-0.200mm	4.09	0.37	4.92	0.37	269.78	15.24	295.20	14.42	359.96	28.81	451.00	52.80
0.201-0.300mm	2.60	0.19	2.49	0.20	46.24	3.19	49.78	3.15	81.22	8.42	78.60	10.14
0.301-0.400mm	6.37	0.43	5.65	0.37	46.56	3.62	49.34	2.94	80.49	8.79	80.12	9.86
>0.400mm	2.15	0.21	2.03	0.24	90.67	6.86	50.29	5.62	119.38	19.02	96.32	19.74

Why seedlings?

- Seed is used in revegetation
- We can look at genetic variation of traits
  - Prerequisite for natural selection
  - Common measurements based on quantitative traits
    - Resemblance of offspring to parents
    - Resemblance among siblings

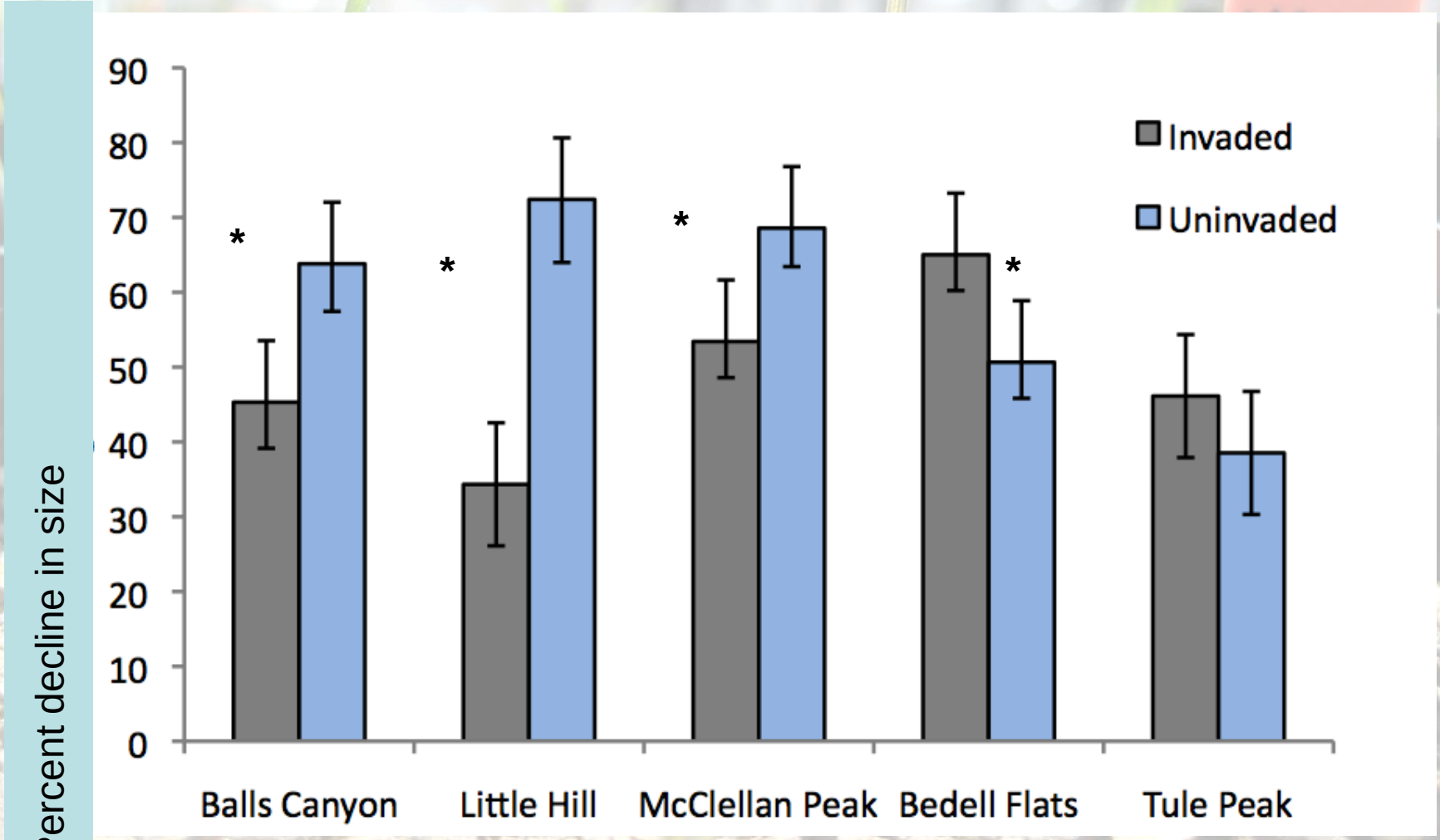






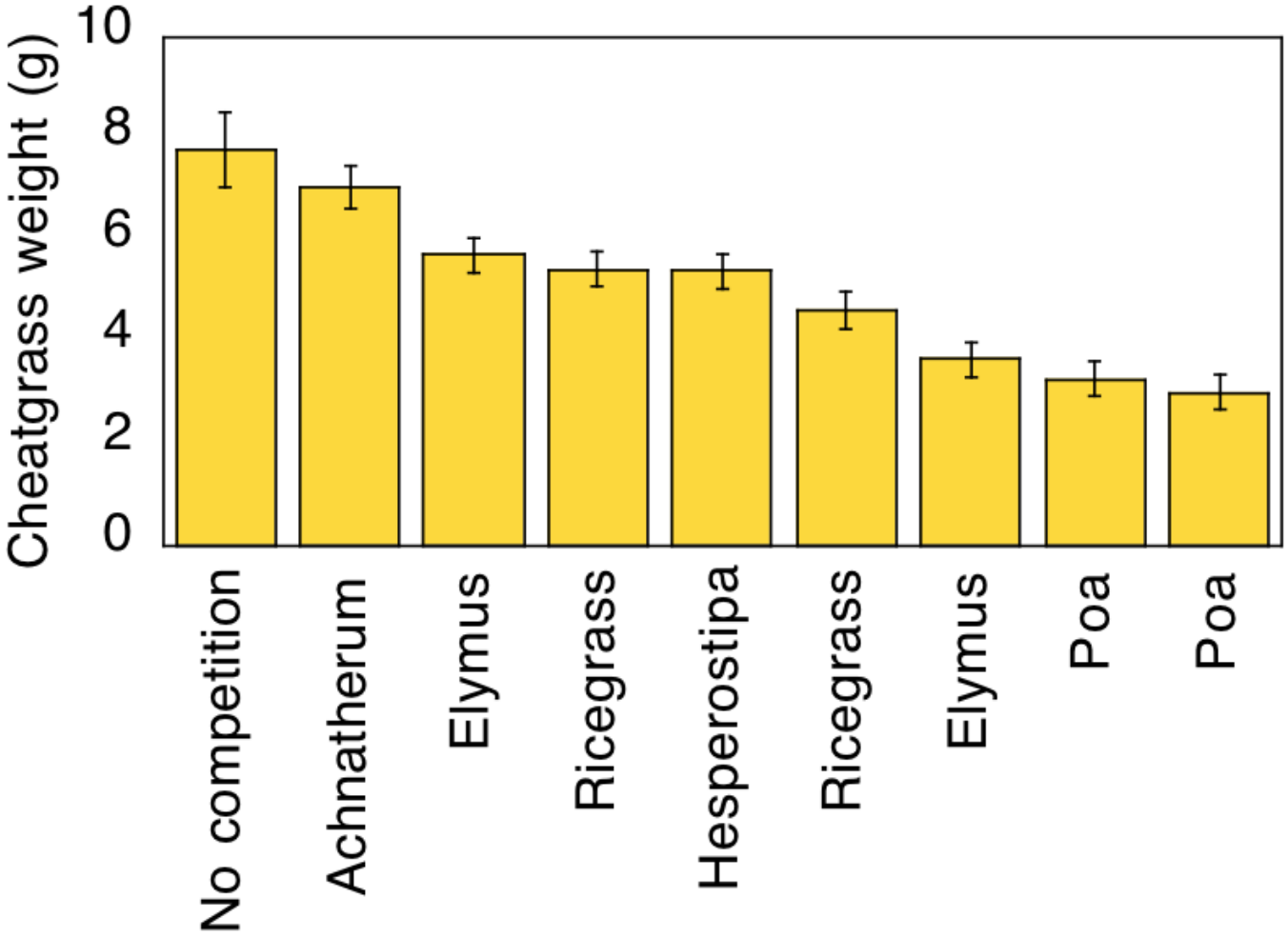
Other Leger Lab
Cheatgrass Competition Research

Three out of five dentists agree



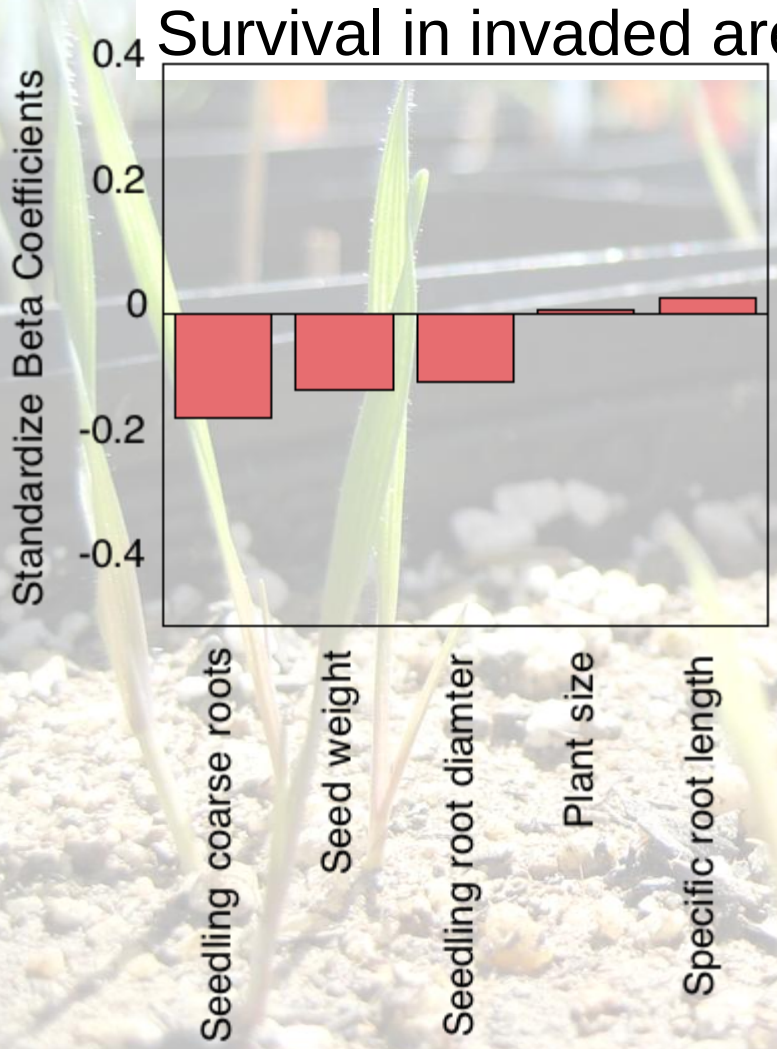
Groegen, Leger, & Espland 2011

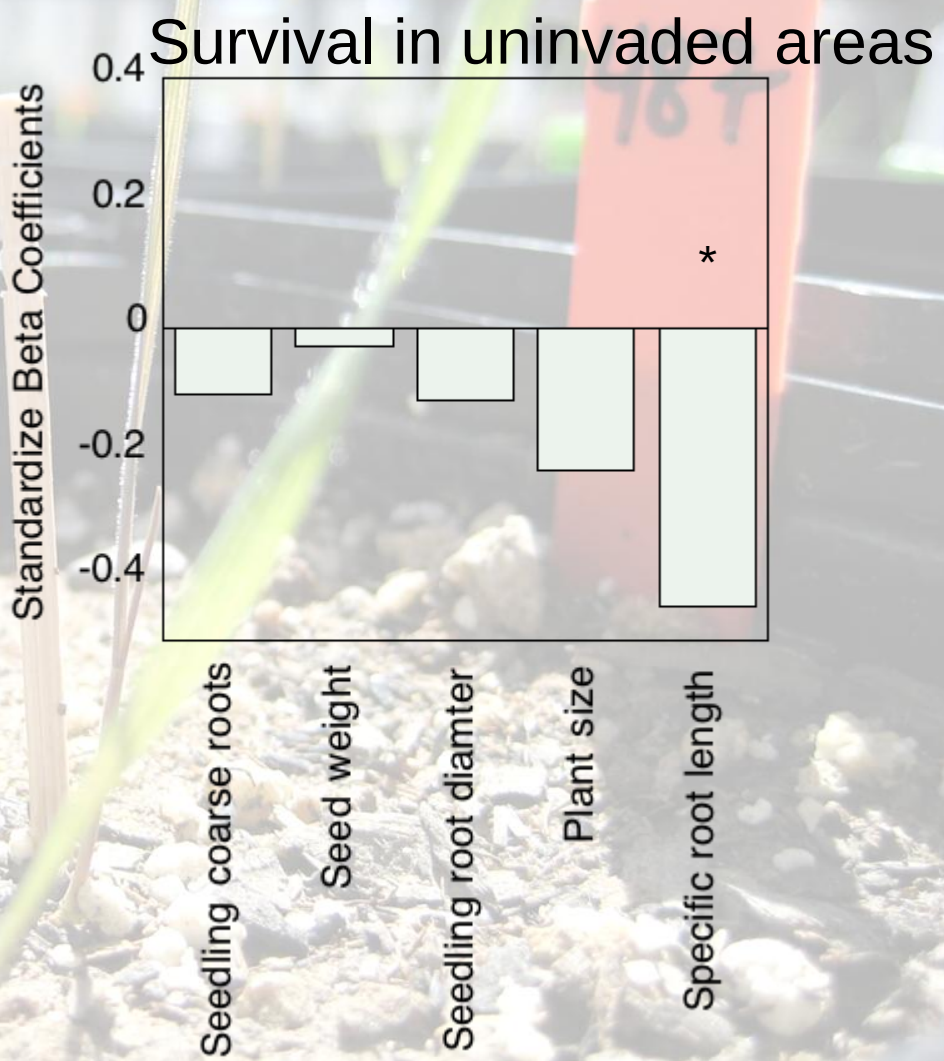
Cheatgrass mass, by species



Groegen, Leger, & Espland 2011

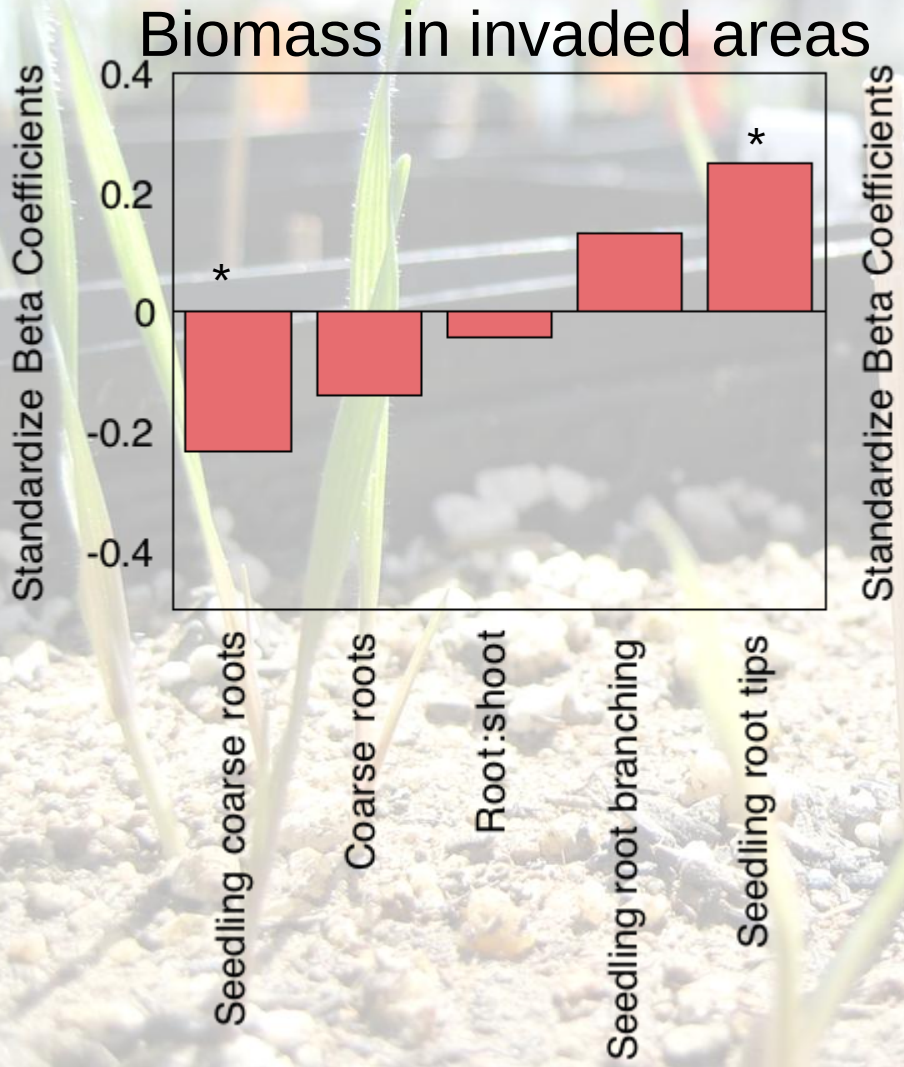
Survival was not well explained by traits we measured

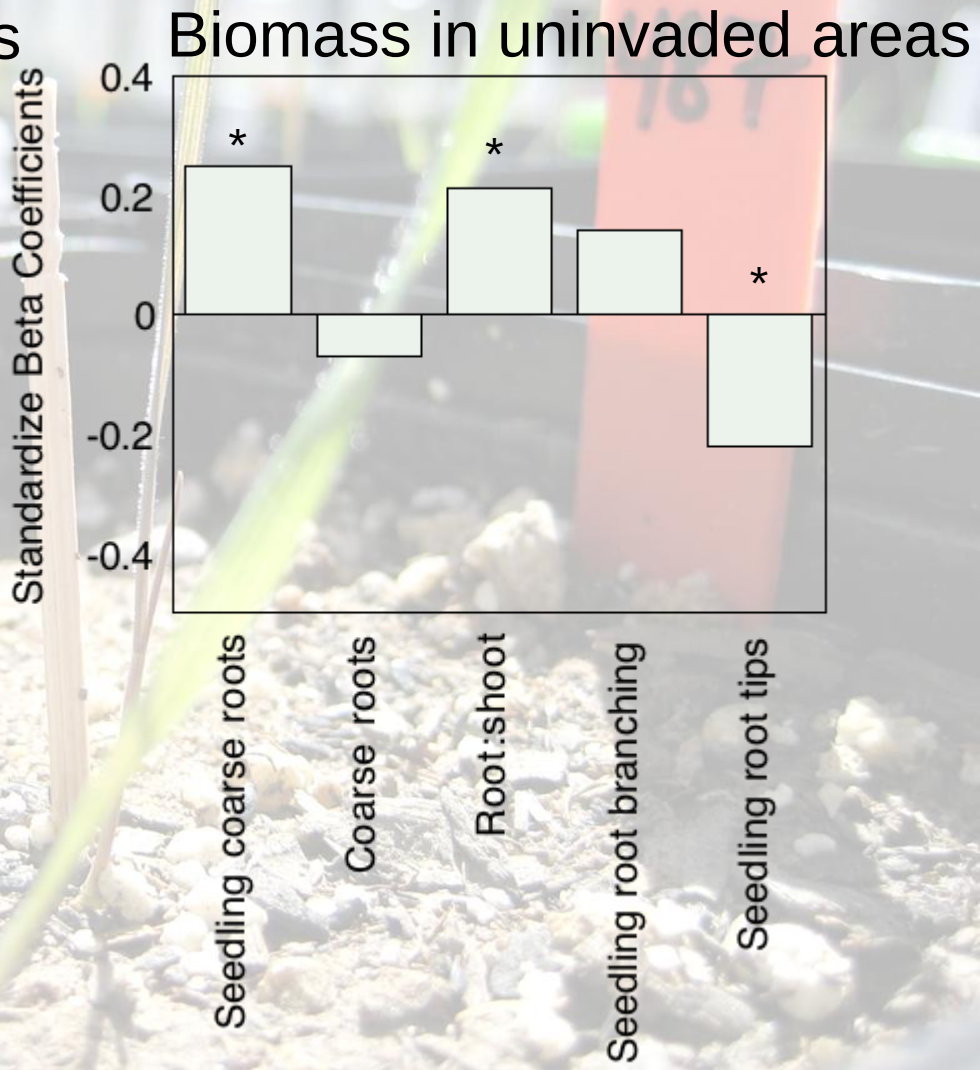




Groegen & Leger, in review

Different traits are important





Several growth traits vary by invasion status

Response Variable	Varies by Invasion Status	Varies by Family	Response Variable	Varies by Invasion Status	Varies by Family
Seed mass (g)	**X**	**X**	50 day root mass (mg)		X
Emergence Date		X	50 day root total root length (cm)		X
Early growth rate (leaf #)	**X**	**X**	50 day root diameter (mm)	X	
Early growth rate (leaf length)	**X**	**X**	50 day root tips		X
50 day leaf #	**X**	**X**	50 day root forks		X
50 day shoot mass (mg)	**X**	**X**	50 day (0.000-0.100mm)		X
50 day total mass (mg)	**X**	**X**	50 day (0.101-0.200mm)		X
100 day leaf #	**X**	**X**	**50 day (>0.400mm)**	**X**	**X**
100 day leaf # with zeroes	**X**	**X**	**50 day % fine roots**	**X**	**X**
100 day shoot mass (mg)	X	--	50 day R:S	X	
100 day total mass (mg)	X	--	100 day root mass (mg)	X	--

In squirreltail plants experiencing cheatgrass competition