**Do non-native plants in the boreal forest benefit more than native species from earlier springs, warmer summers or extended autumns?**

Christa P.H. Mulder and Katie V. Spellman, University of Alaska Fairbanks

The boreal forest of Interior Alaska is experiencing rapid warming: The number of days in summer during which temperatures remain above freezing has increased by 45 percent (from 85 to 123 days) in the past 100 years. We evaluated whether earlier springs, warmer summers, and extended autumns provide an advantage to non-native plants by tracking the phenology of 39 plant species (27 native and 12 non-native) in three sharply contrasting years. Compared to long-term averages, 2013 had a very late spring, warm summer, and a greatly extended autumn, 2014 a moderately early spring, cool summer, and average autumn, and 2015 a very early spring, average summer, and short autumn. Native plants had significantly earlier dates of first flower, peak flowering, and first leaf and peak leaf production than non-native plants, and flowering was advanced in both groups in the early spring year compared to the late spring, but there was no difference in the size of the shift between native and non-native species. Developmental times (e.g., from peak flower to half of fruits ripe) were shorter for native species than for non-native species but did not differ between years. Non-native plants produced their last leaf later than non-natives, but this difference was much greater in 2013 (extended autumn: 52 days) than in years with an average autumn (2014: 8 days). Similarly, senescence of non-natives was delayed by two weeks in 2013 compared to natives, but concurrent in 2014. Non-native species also extended their flowering period beyond that of native species, and more so in 2013 than 2014 or 2015, but this did not result in extended fruit production. We found no evidence that earlier springs or warmer summer gave an advantage to non-native species, but extended autumns may benefit non-native species more than native species by prolonging leaf production and retention.

# Do non-native plants in the boreal forest benefit more than native species from earlier springs, warmer summers or extended falls?

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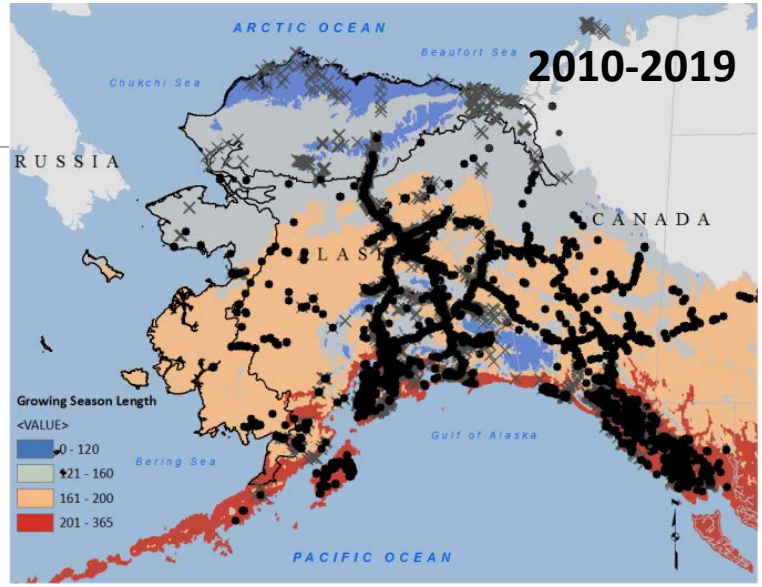
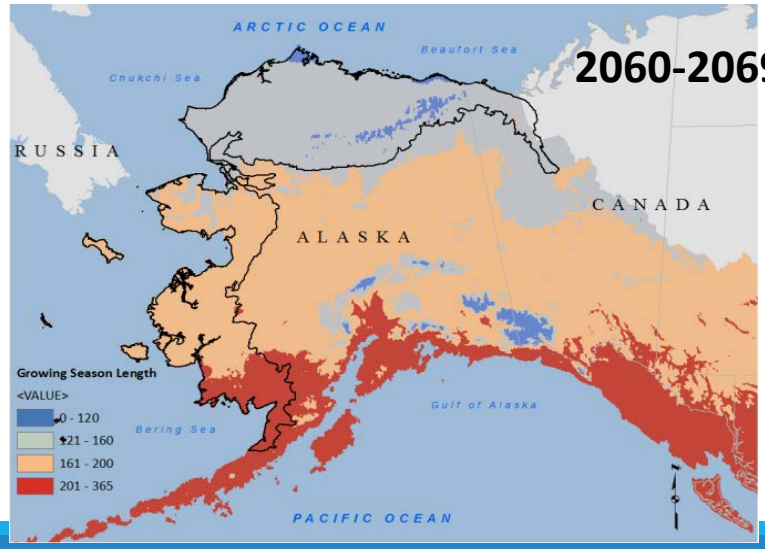
# Climate change in interior Alaska

- In interior Alaska, climate change has led to earlier springs (e.g., earlier date of snowmelt), warmer summers, and later falls (e.g., later date of freeze-up)
  - This has resulted in a 45% increase in above-freezing days in the past 100 years (from 85 to 123 days)
- Predictions are for continued warming, resulting in longer growing seasons across the state

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# Gut feeling: warmer summers favor non-natives

- There is an overall sense among both scientists and the general public that longer, warmer summers give non-natives an edge
- There is a general sense that longer <u>falls</u> in particular favor non-native plants: some non-natives stay green until the snow hits

Three non-native species in October 2016

# Conditions for successful expansion

For a non-native plant to successfully expand in a new area it needs to:

1. Be able to survive the physical conditions
2. Compete successfully with native species
3. Have access to mutualists

Warmer temperatures and longer seasons may also benefit native species

- If this benefit is as large (or larger) for native species, then non-natives may not gain an edge

- Warmer temperatures and longer seasons may affect non-survival but not provide a competitive advantage
- Currently, we have no clear understanding of what aspects of climate change (if any) **provide a competitive advantage** to non-native species

# Earlier springs

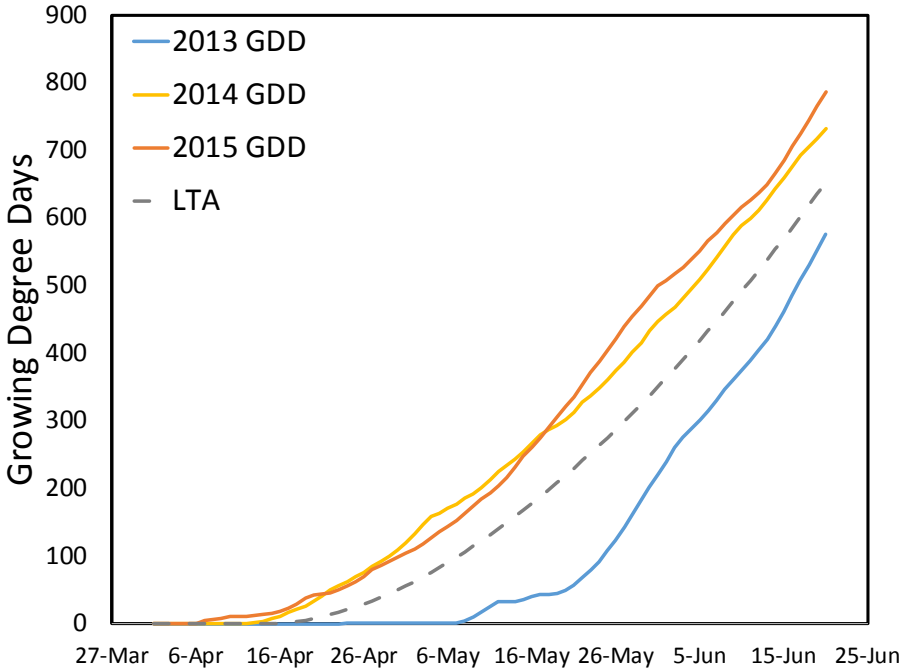
Selection for rapid starts in native plants:

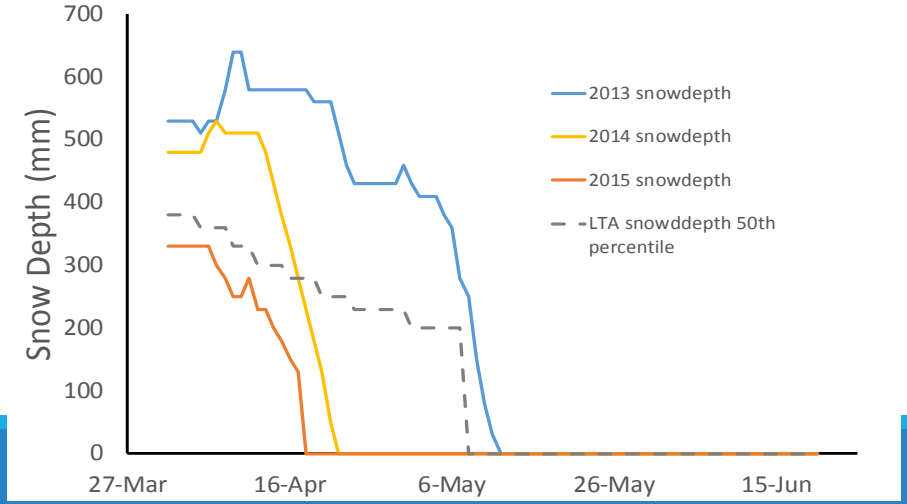
- Boreal forest plants preform buds at leas 1 year prior to flowering or leafing out

- Timing of budburst is likely limited by ground thaw
- Leaf and flower production tends to be rapid and highly synchronous

Native species may be more able to respond to early springs than non-native species

- Spring of 2013 was very late
- Spring of 2014 was intermediate
- Spring of 2015 was very early

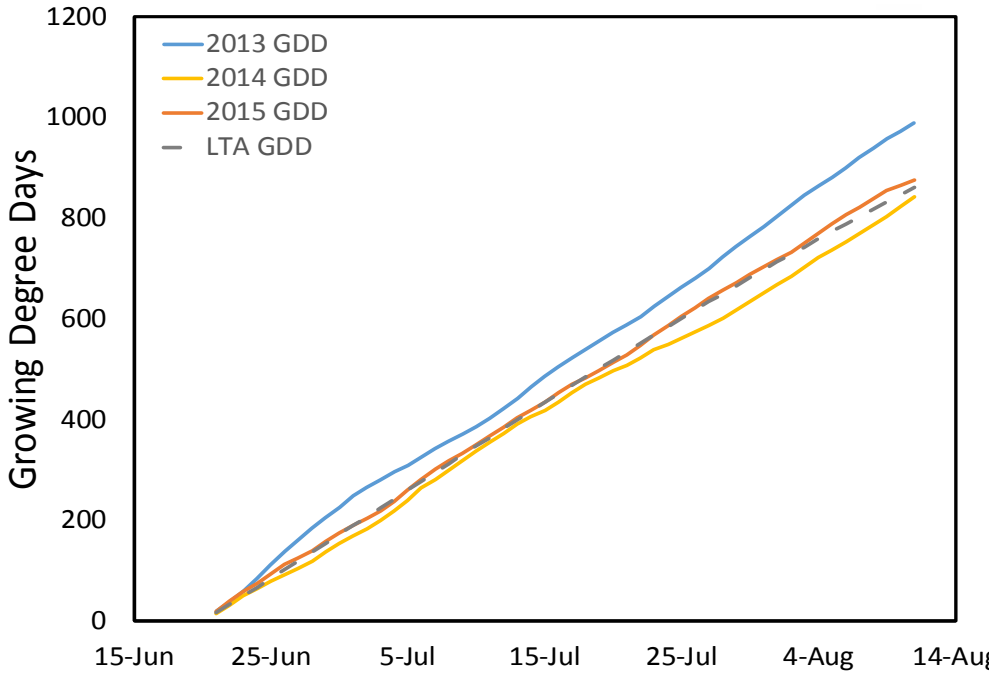


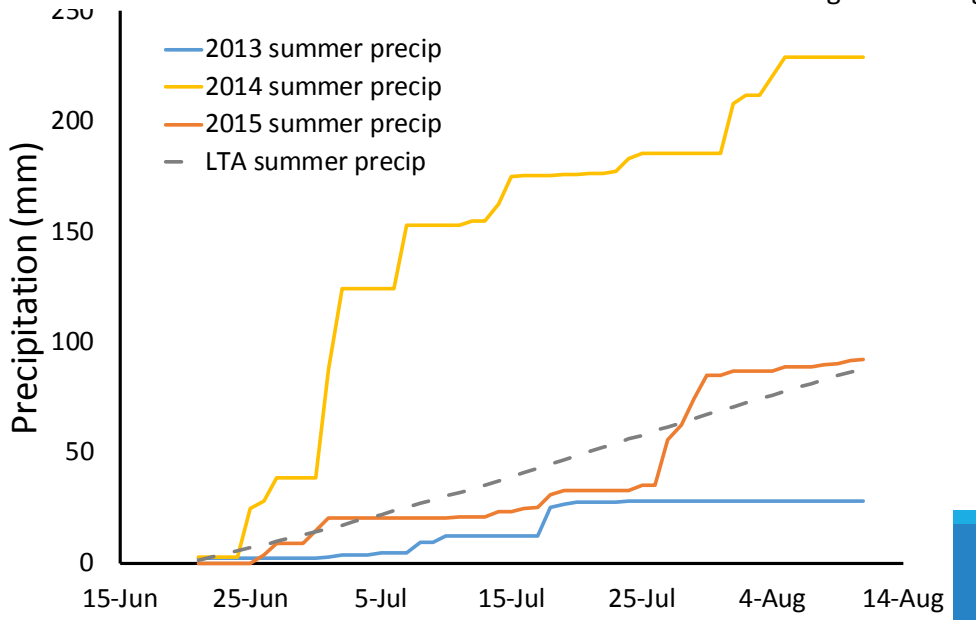



# Warmer summers

- Warmer temperatures are likely to lead to faster development in all species
- However, ability to respond may differ between plants with different traits (e.g., forbs vs. evergreen shrubs), which may favor non-native species

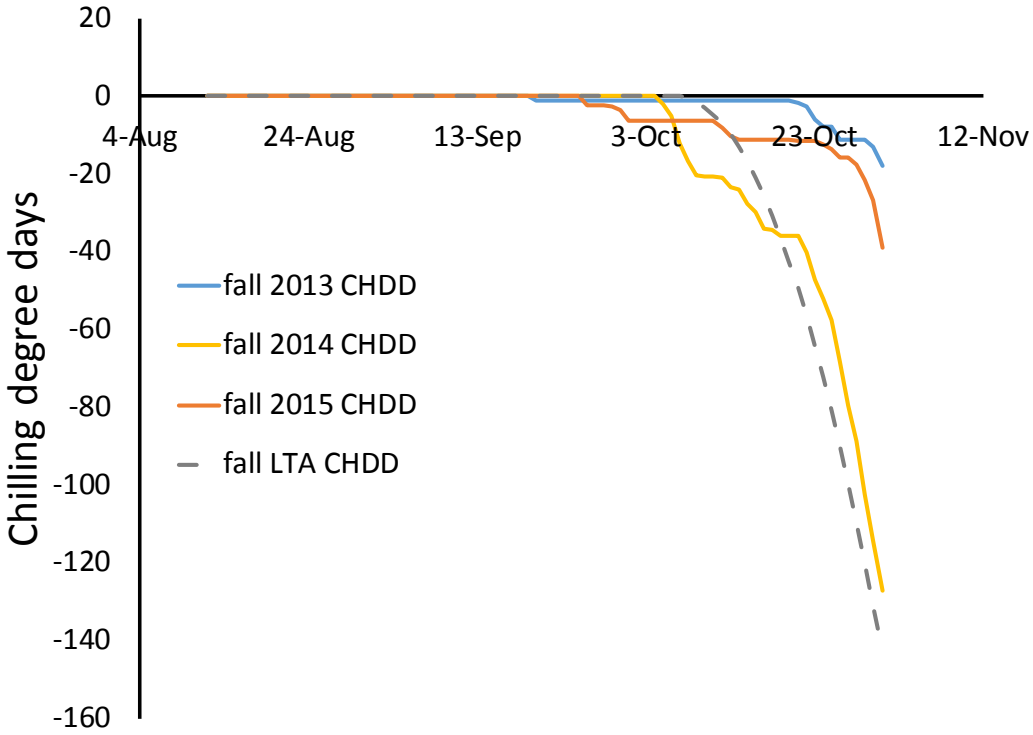
- Summer of 2013 was hot and dry
- Summer of 2014 was slightly cool and wet
- Summer of 2015 was average



# Later falls

- Selection for a conservative strategy may have led to early senescence in native species regardless of temperature (e.g., cued by photoperiod)
- If non-natives are cued by temperature, this may give them an advantage under extended falls

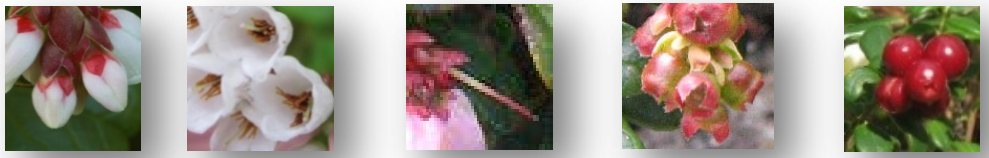



- 2013 had a very extended fall
- 2014 was close to average
- 2015 had an early end of fall

# Methods: Retro Science

**Data Collection**:

- We selected 27 native and 12 non-native insect-pollinated species
- In 2013, 2014 and 2015 we marked 5-10 individuals of each species, and on a weekly basis:
  - Counted the number of reproductive units in bud, flower, “petal-drop”, unripe fruit, or ripe fruit stage



  - Counted the number or percentages of emerging, unfurled, or senescing leaves

Katie Spellman with (from top) Patricia Hurtt, Katie Moeller, Brendan McKinnon and Marcy Kuntz

# Methods: species

Native species included:

Evergreen shrubs (4)

Deciduous shrubs (6)

Deciduous forbs (14)

Wintergreen forbs (3)

Non-native species included:
Forbs (10)
Deciduous shrubs (2)

# Methods: analysis

We used ANOVA to test for:

- Differences between years
- Interaction between year and native status
- Species identity was included in the model

- We tested for differences between native and non-native species using means across the 3 years (to prevent pseudo-replication)
- Where we found differences between native and non-native species, we tested for differences within deciduous forbs or within families

# Hypotheses

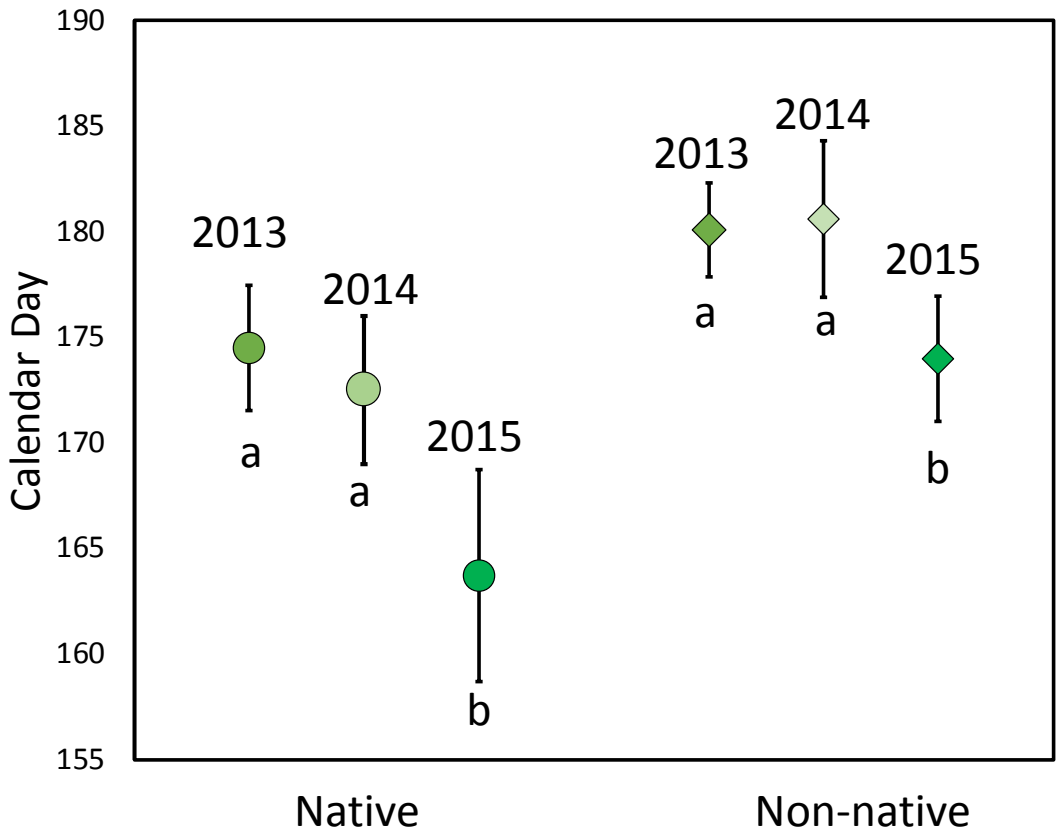
| Climate variable | Response variable | Null # 1: No effect | Null #2: equal effect | Alt #1: Advantage to non-natives | Alt #2: Advantage to natives |
|---|---|---|---|---|---|
| Earlier spring | Flower production | | | | |
| Earlier spring | Leaf production | | | | |
| Warmer summer | Development rate of fruits | | | | |
| Later fall | Production of last flower and fruit | | | | |
| Later fall | Production of last leaf | | | | |
| Later fall | Retention of leaves | | | | |

NA = native, NN= non-native

# First Flower

2013= late spring
2014=early spring
2015= very early spring

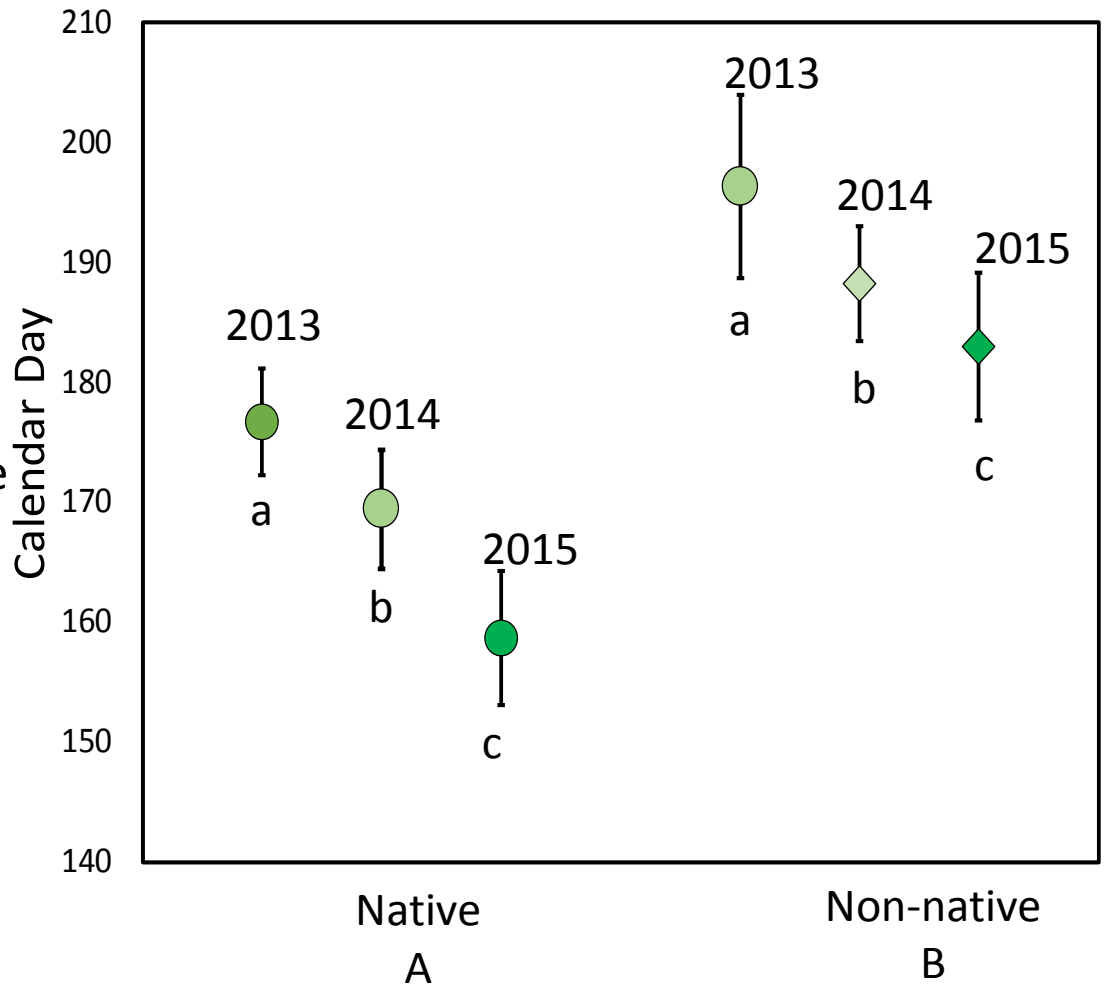
- Native plants produced their first flower earlier than non-native plants (but this difference was not significant when means per year were used)
- All plants produced their flowers earlier in 2015 than in 2013 or 2014 (P<0.001)
- Shifts between years were the same for native and non-native plants (no interaction: P=0.44)



# Peak Flower

2013= late spring
2014=early spring
2015= very early spring

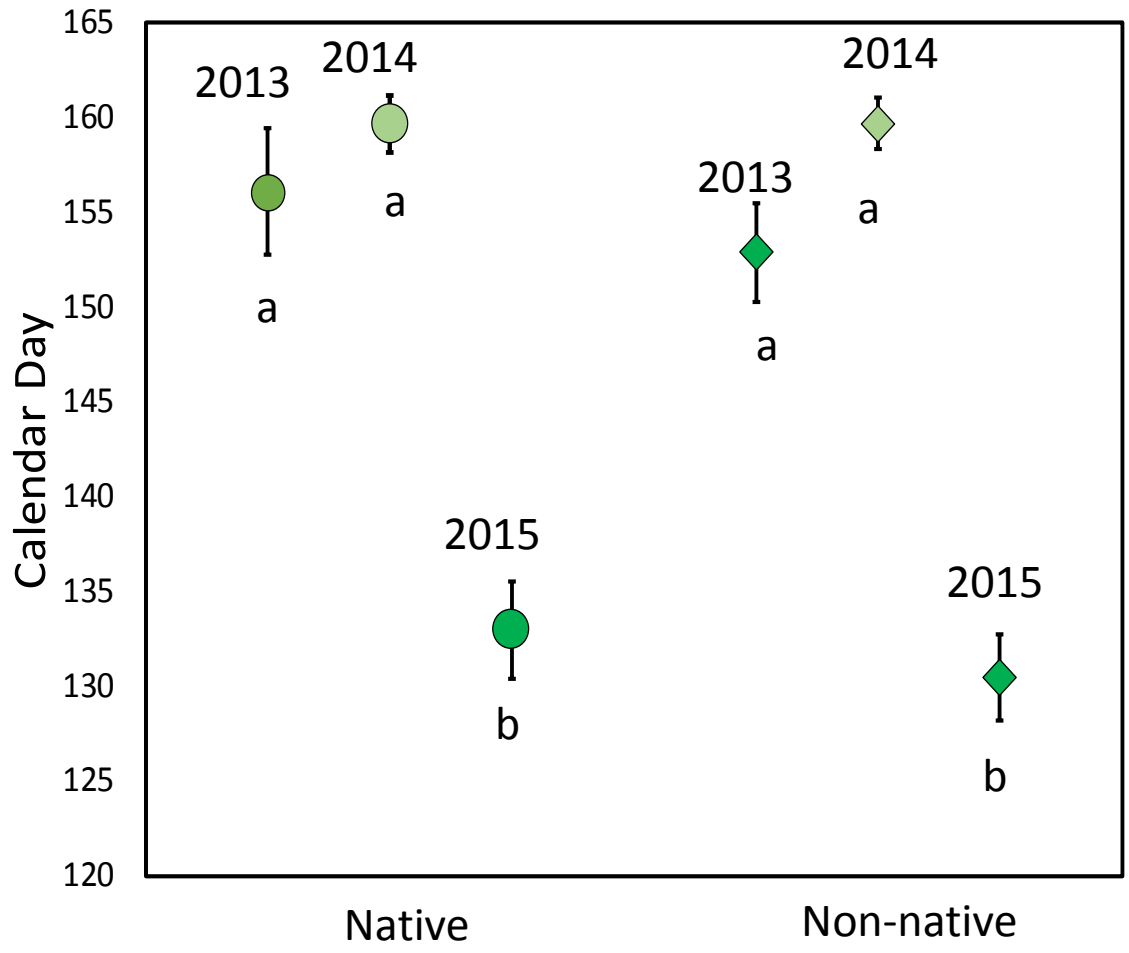
- Native plants reached peak flowering earlier than non-native plants (for means: P=0.024)
- All plants reached peak flowering earliest in 2015 and latest in 2013 (P<0.001)
- Shifts between years were the same for native and non-native plants (no interaction: P=0.54)
- The difference in patterns between first flower and peak flower can be explained by greater synchrony in native plants (P<0.001)



# First Leaf

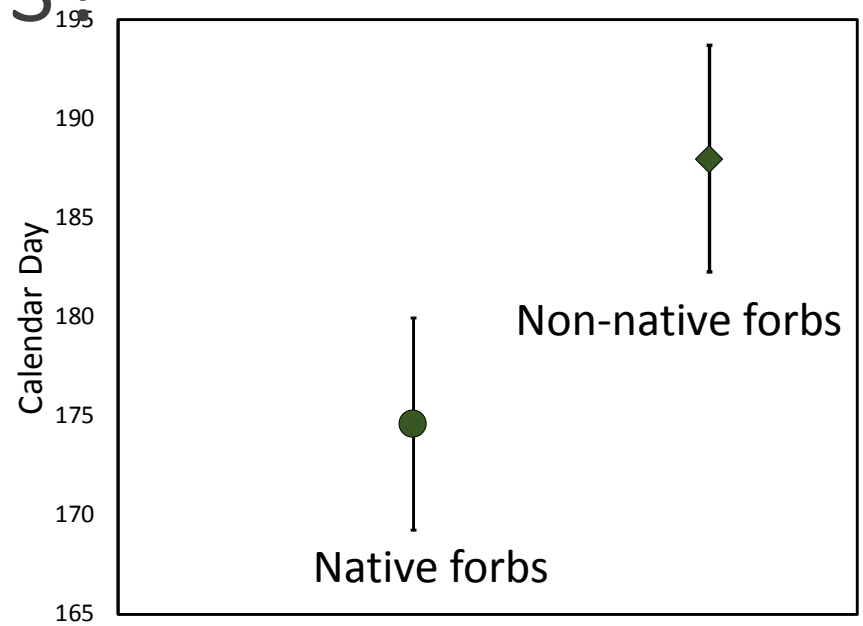
2013= late spring
2014=early spring
2015= very early spring

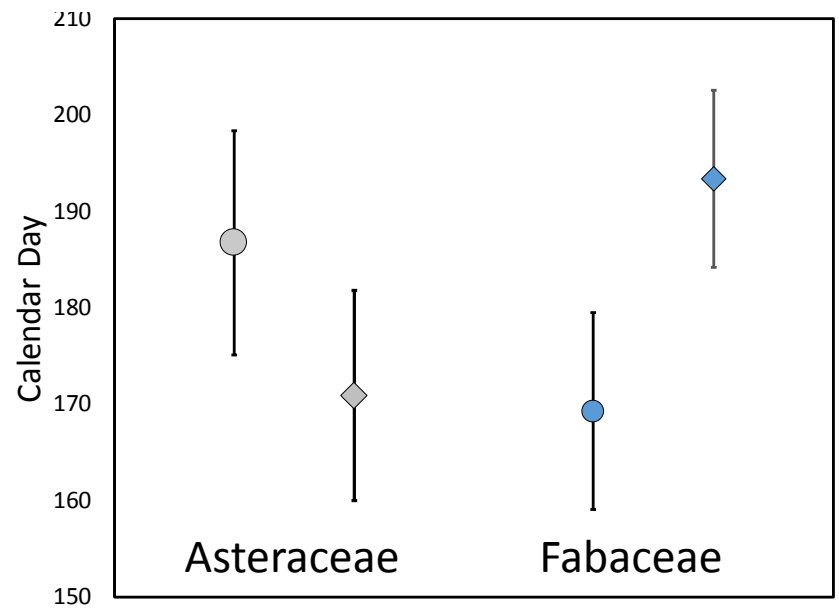
- There was no difference in date of first fully expanded leaf between native and non-native species (P=0.74)
- First leaf production was earlier in 2015, than in the other 2 years
- Shifts between years were the same for native and non-native plants (interaction: P=0.54)



# Why do non-natives flower later than natives?

- Forbs reach peak flowering later than shrubs (P<0.01)
- Deciduous and wintergreen plants tend to flower later than evergreen plants (P=0.10)
- But when comparing only deciduous forbs, there is still some evidence that non-natives flower later (P=0.098)
- Can phylogeny (family) explain the difference?
  - YES: There are no consistent differences between native and non-native plants within families



# Support for Hypotheses: Earlier Springs

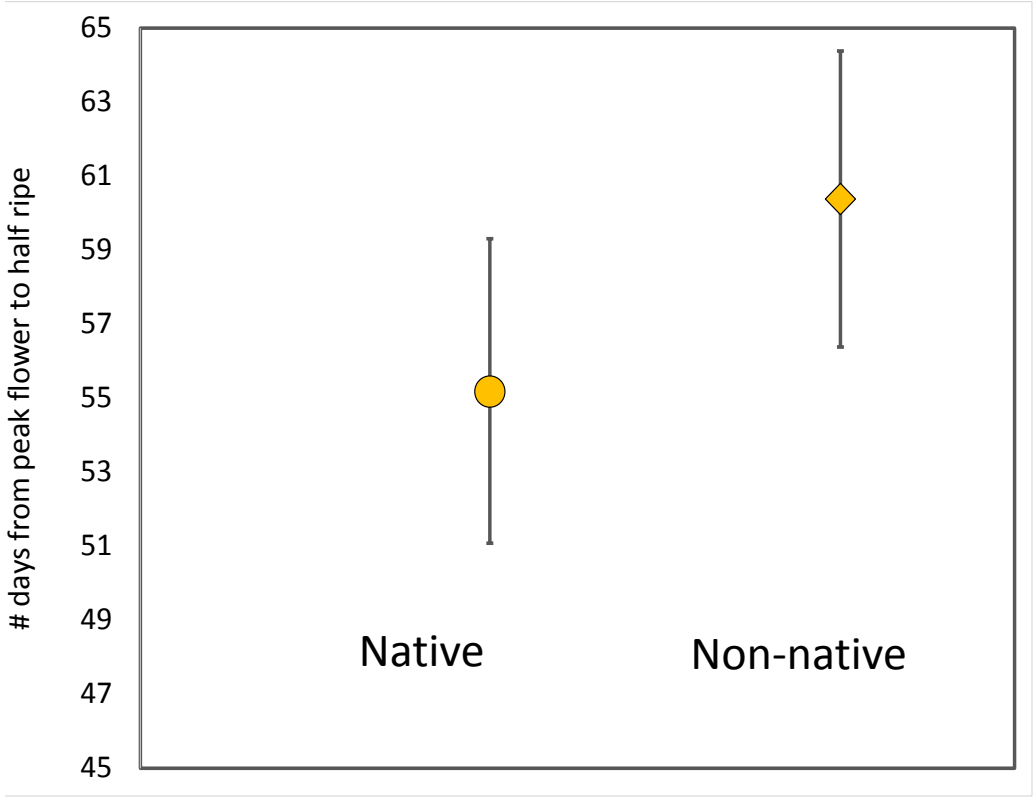
| Response variable | Phenology means of natives vs non-natives | Null # 1: No effect | Null #2: equal effect | Alt #1: Advantage to non-natives | Alt #2: Advantage to natives |
|---|---|---|---|---|---|

NA = native, NN= non-native

# Developmental rates

- No differences between native and non-native species in
  - #days from 1st flower to 1st unripe fruit
  - # days from 1st unripe fruit to 1st ripe fruit
  - # days from peak flower to half ripe fruits
- Only marginally significant differences between years for 1st flower to 1st unripe, or 1st unripe to 1st ripe fruit (development was 6-7 days faster in 2013 than in 2015; P<0.1)
- No difference between years in days from peak flower to half ripe fruits (P>0.7)
- No significant interactions for any of these variables

2013= warm summer
2014=cold summer
2015=average



# Support for Hypotheses: Warmer summers

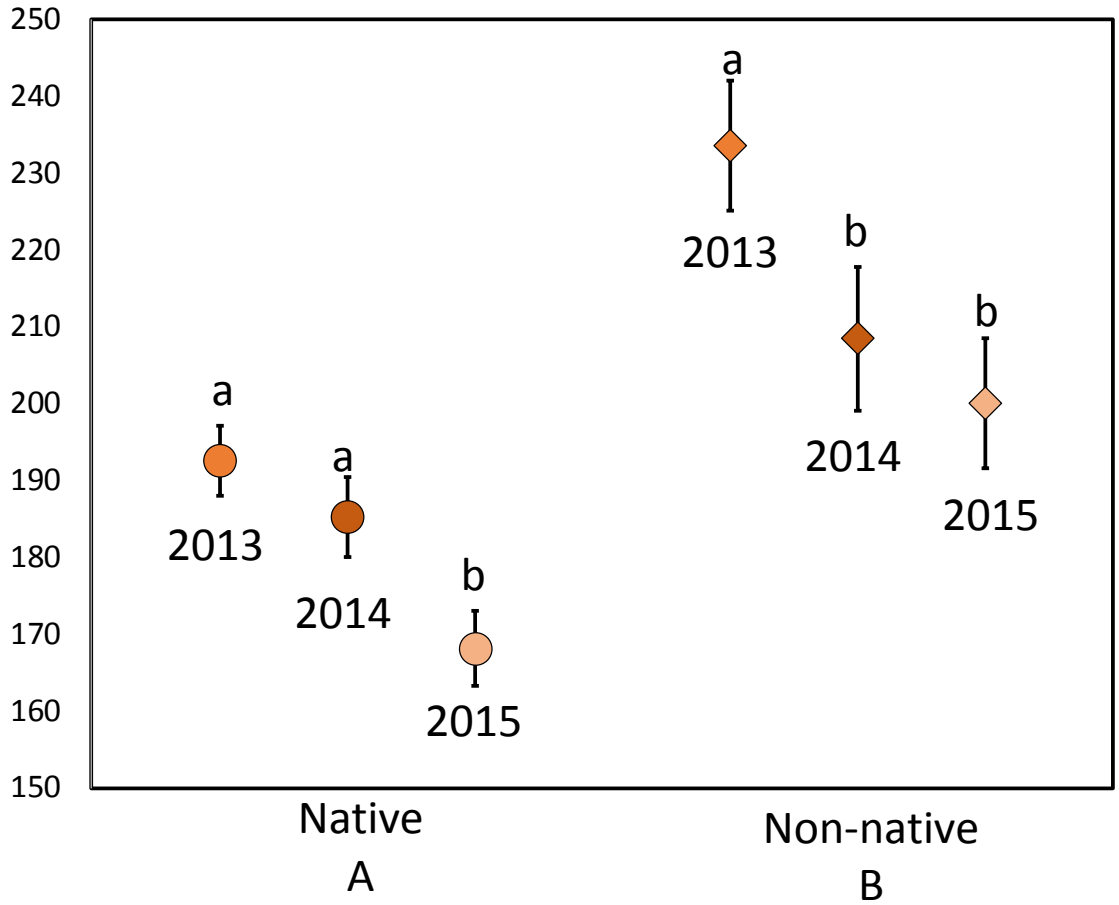
| Response variable | Phenology means of natives vs non- | Null # 1: No effect | Null #2: equal effect | Alt #1: Advantage to non-natives | Alt #2: Advantage to natives |
|---|---|---|---|---|---|

NA = native, NN= non-native

# Production of last flower

2013=late fall
2014=average fall
2015=early fall

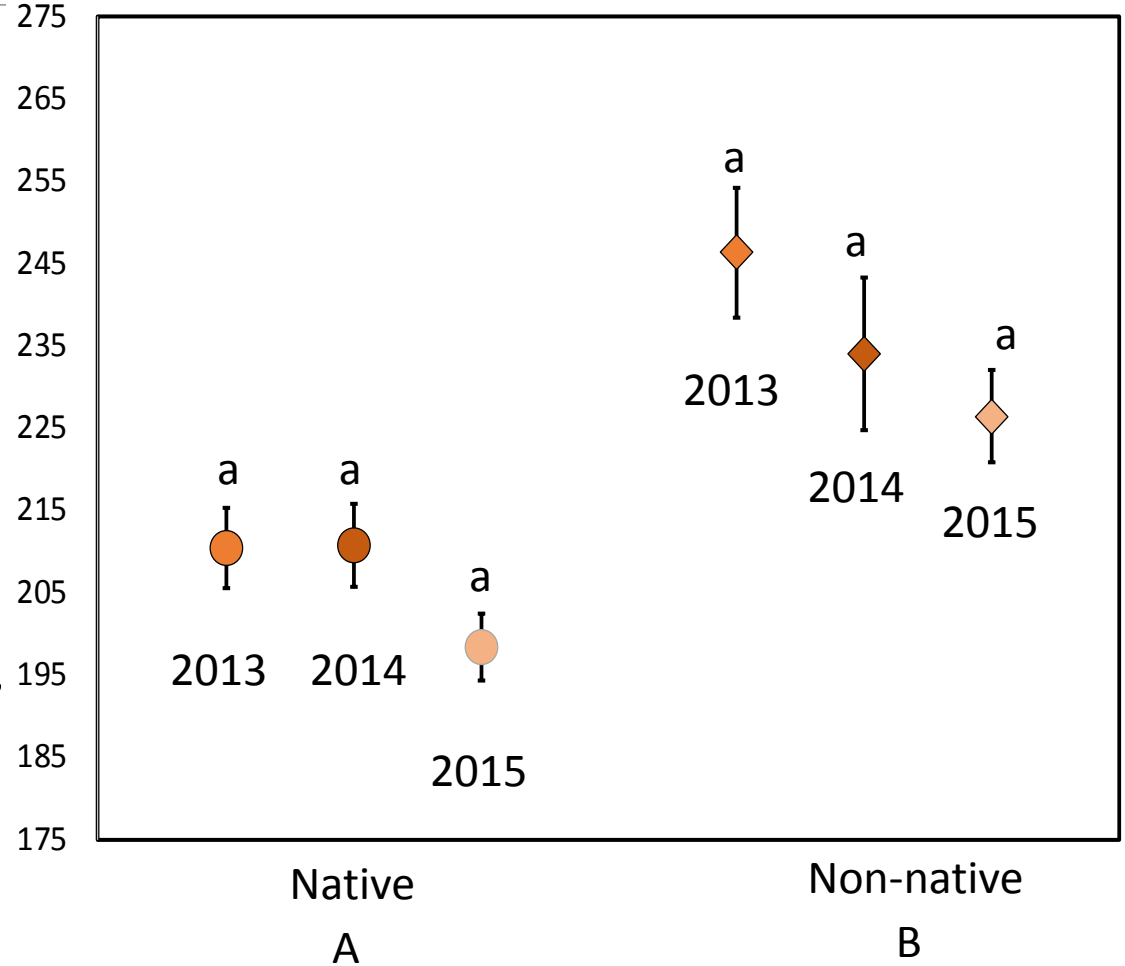
- Non-native plants produced their last flower later than native plants (P<0.001)
- There were large differences between years, with the latest cessation of flower production in 2013 and the earliest in 2015
- There was a significant interaction between year and native status: shifts between years were much larger for non-native species than for native species

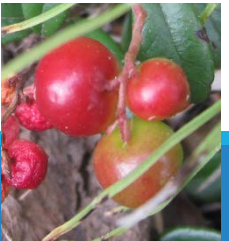


# Production of last unripe fruit

2013=late fall
2014=average fall
2015=early fall

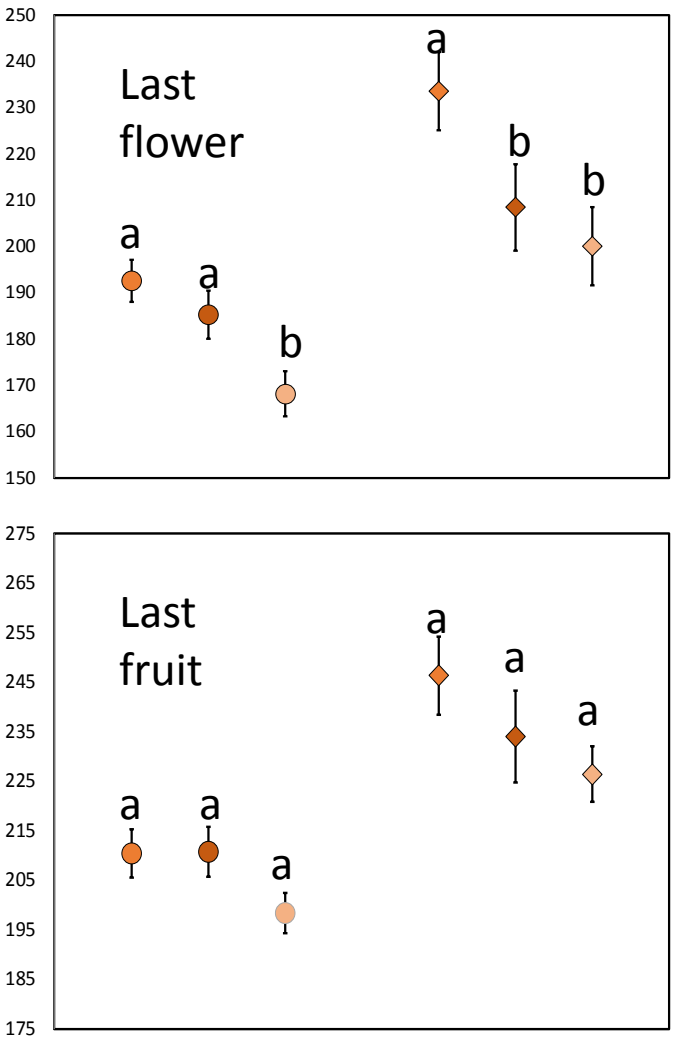
- Non-native plants produced their last unripe fruit later than native plants (P<0.001)
- There were differences between years, with earlier cessation of fruit production in 2015 than in the other two years
- However, there was no interaction between year and native status: the shift between years was the same for native as for non-native plants (P=0.24)
- When only forbs were examined, native plants actually produced the last fruit LATER (by 13 days)



# Why do last flower and last fruit respond differently to inter-annual variation?

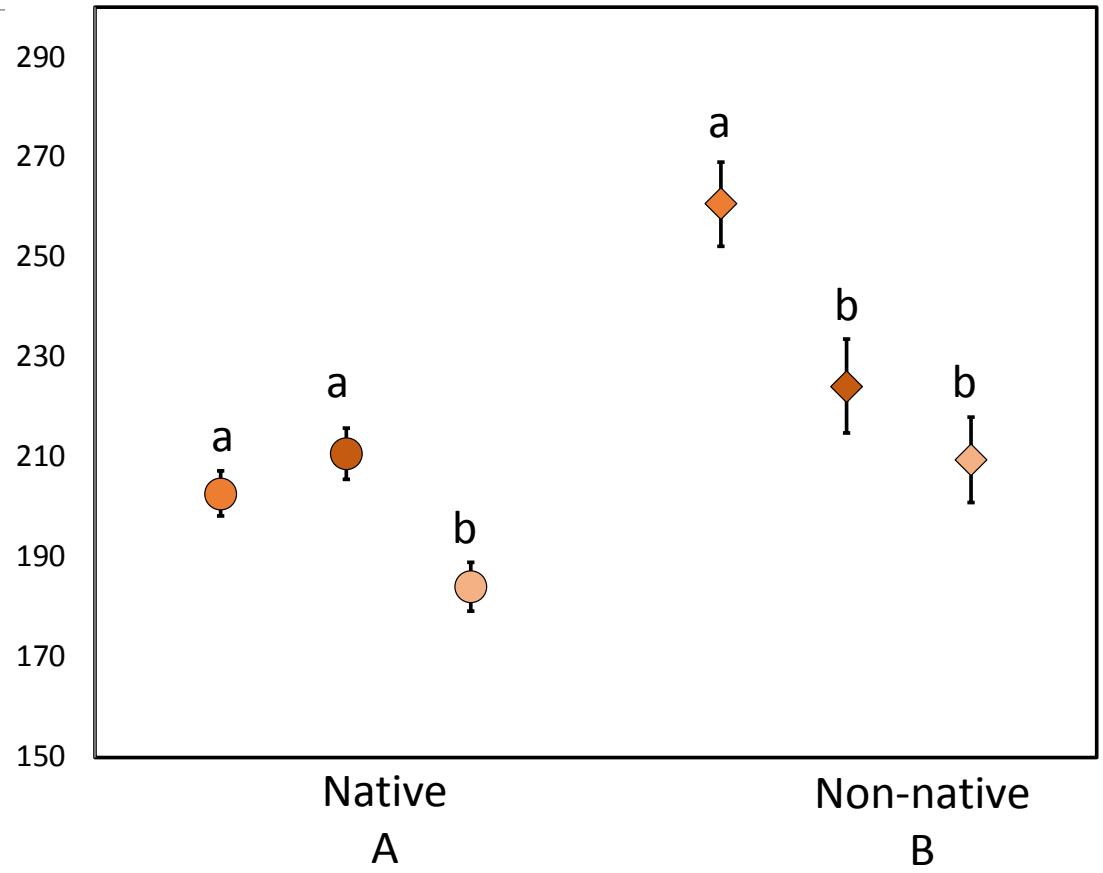
- Native plants stopped **producing** flowers and fruits earlier in the early-start year (2015) but did not extend production in the late-end year (2013)
- Non-native plants did not show a difference between the early-start year (2015) and the average year (2014), and continued to produce flowers much later in the late-end year (2013). However, they did not extend fruit production in the late-end year.
- Possible explanation: no pollinators!



# Leaf production

2013=late fall
2014=average fall
2015=early fall

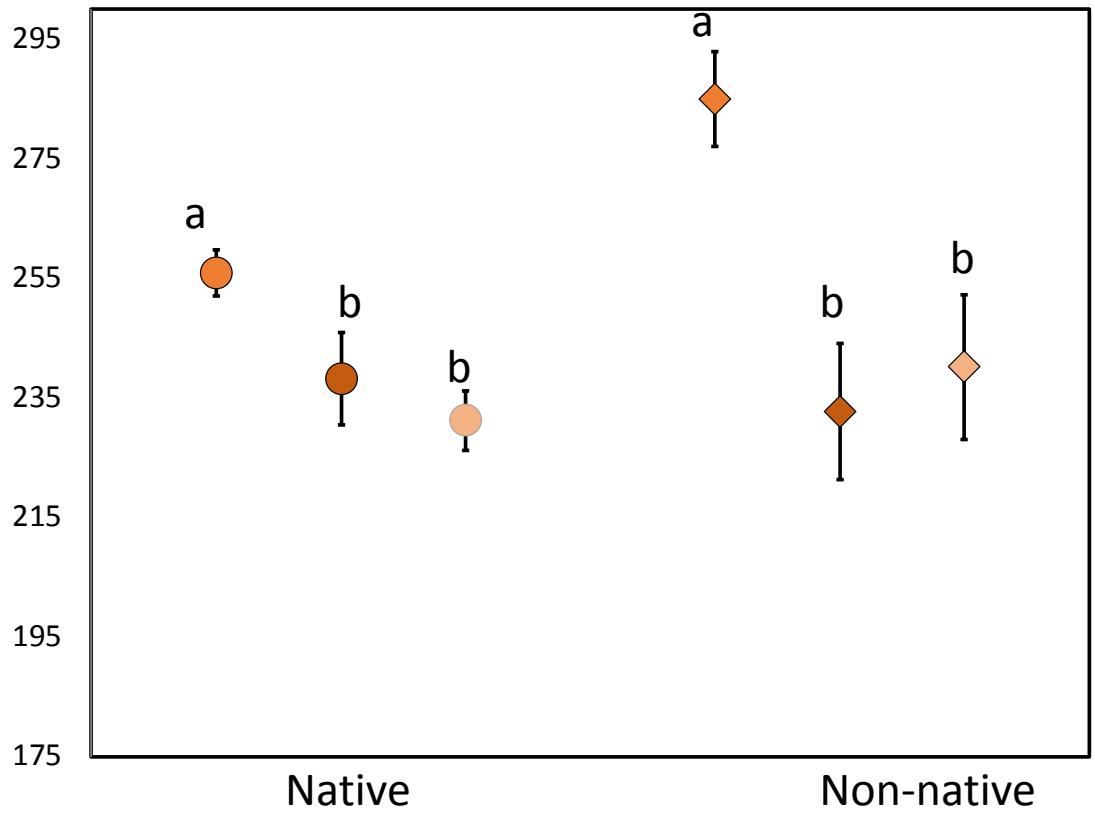
- Non-native plants produced their last leaf later than native plants
- There were large differences between years, with earlier cessation of leaf production in 2015 than in 2013 or 2014
- There was a significant interaction between year and native status (P<0.001): native species did not extend leaf production in the late-fall year, but non-native species did
- When comparing only forbs, non-native species stopped leaf production 32 days after native forbs (P=0.003)



# Leaf 50% senescence

- Native and non-native plants did not differ in mean time of senescence
- There were large differences between years, with later senescence in 2013 than in 2014 or 2015
- There was a marginal interaction between native status and year (P=0.070): the delay in senescence in 2013 was greater for non-native plants than for native plants (P=0.050)

2013=late fall
2014=average fall
2015=early fall



# Support for Hypotheses: Later Falls

| Response variable | Phenology means of natives vs non-natives | Null # 1: No effect | Null #2: equal effect | Alt #1: Advantage to non-natives | Alt #2: Advantage to natives |
|---|---|---|---|---|---|

NA = native, NN= non-native

# Summary and Caveats

- No evidence for an advantage for non-natives in spring or summer: both show similar responses to earlier springs and warmer summers
- Non-native plants continue to produce flowers longer than native plants in a late fall… but in the absence of later fruit production this is a <u>disadvantage</u> to non-natives!
- Non-native plants produce leaves for longer, even after controlling for growth form…. This does appear to be a real advantage in terms of productivity.
- But...
  - Whether these late leaves "pay for themselves" is unknown
  - Evergreen and wintergreen native species continue to photosynthesize into the fall
- We compared 3 years with similar total growing degree days (2120, 2100, and 2090 resp.). We don't know what would happen if a year started earlier AND was warmer AND continued late
- We don't know what will happen to pollinator communities over time

# Thanks to….

- Volunteers, technicians, interns and RET Teachers: Patricia Hurtt,  Brendan McKinnon, Marcy Kuntz, Katie Moeller
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- Support: Bonanza Creek LTER

…and to all of you for your attention