Adaptation of Forest Trees to Climates, Consequences for Climate Change, and Management Responses

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Main points:

1. Plant species and populations are adapted to some climatic niche, usually locally adapted.
2. Climates are changing, which affects adaptedness. Therefore, choice of species and populations matter for the future health and productivity of forest stands.
3. We can manage genetic variation to positively influence how plants respond and adapt to climate change.

Point #1

Plant species and populations are adapted to some climatic niche, usually locally adapted.

Adaptation - Definitions

- The evolutionary process whereby a population becomes better suited to its environment
- A feature which is especially important for an organism's survival and reproduction; a product of natural selection in a given environment (adaptive trait)
  - Heritable
  - Functional
  - A result of natural selection
- Adaptedness is the state of being adapted: the degree to which a population of organisms is able to survive, grow and reproduce in a given environment

Other definitions of adaptation

More broadly in biology: the capacity for an organism to adjust to varying environmental conditions

- More properly termed flexibility, acclimatization, or phenotypic plasticity

"Societal" adaptation: the adjustment of natural or human systems to new environments, which moderates harm or exploits opportunities (IPCC 2001)

How do scientists study adaptation?

Evidence for adaptation comes from:

1. Correlation between a character and environmental factors (genecology studies)
2. Comparisons of naturally-occurring variants in environments where they are hypothesized to function as an adaptation (reciprocal transplant studies)
3. Watching natural selection in action – e.g., peppered moth in England, pesticide resistance
4. Direct evidence from altering a character to see how it affects function in a given environment
5. In population genetics, deviation of genetic differences from what would be expected from neutrality (F_{ST} outliers, Tajima's D)

Studying Genetic Variation

Common-garden experiments are used to separate genetic from environmental effects

$$\mathbf{P = G + \cancel{E}}$$

Environment is more uniform

- "E" is smaller
- Phenotype (P) more closely reflects the genotype (G)

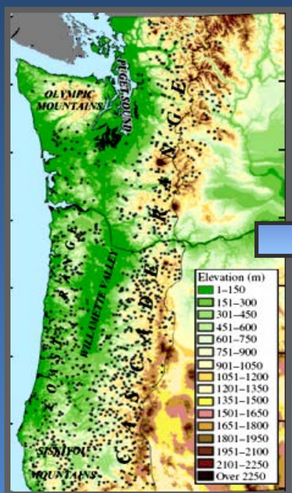
Genecology Studies

- The study of intraspecific genetic variation of plants in relation to source environments (Turresson 1923)
- Seeks correlations between “plant type” and “habitat type”
- Consistent correlations are taken to indicate adaptation as determined by natural selection

Douglas-Fir Genecology Study

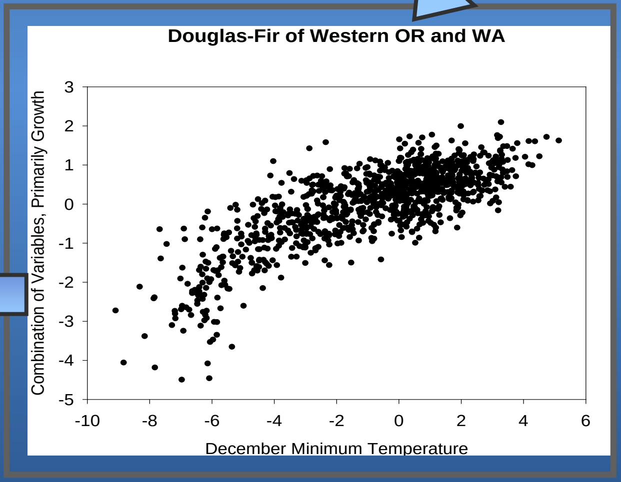
(Pseudotsuga menziesii var. menziesii)

Collect seed from many trees



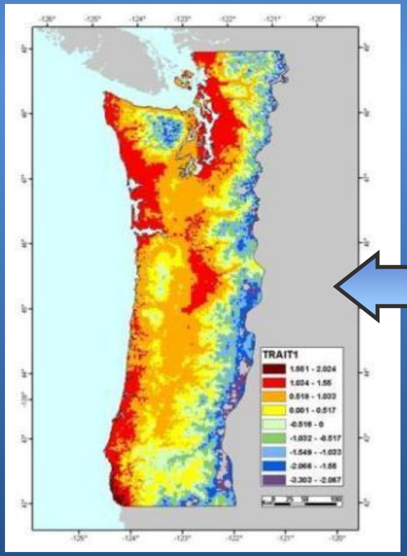
Grow families in a common environment

Measure many adaptive traits



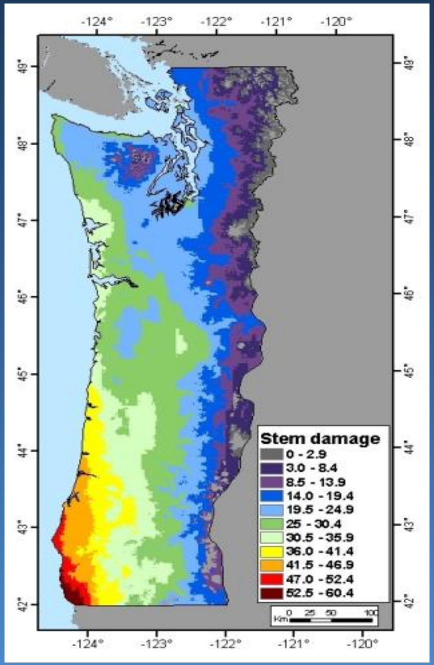
Traits vs source environment

GIS



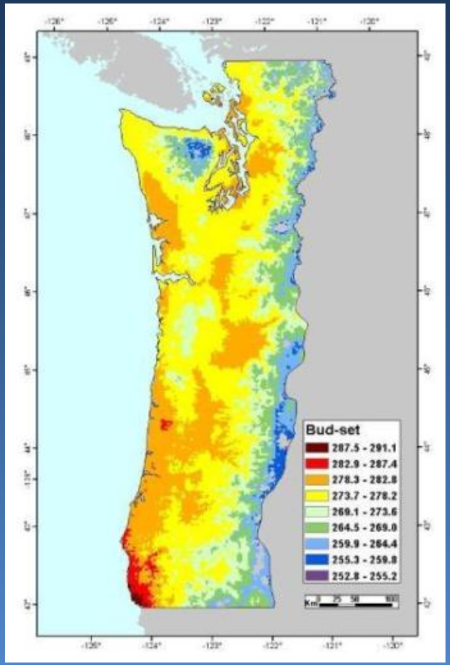
St.Clair et al. 2005. Genecology of Douglas-fir in western Oregon and Washington. Annals of Botany 96: 1199-1214.

Fall cold damage



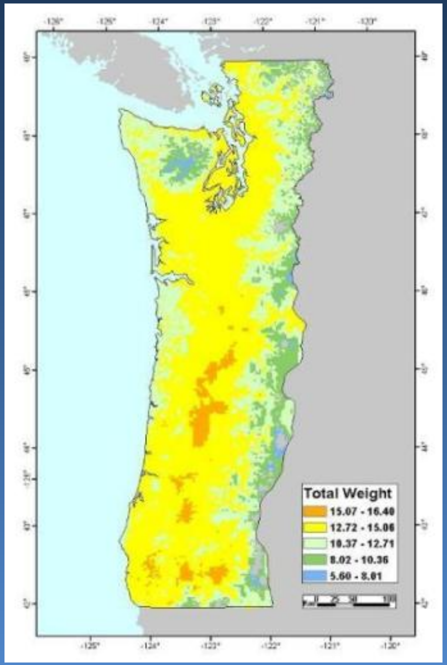
r = 0.79
Qst = 0.68

Bud-set



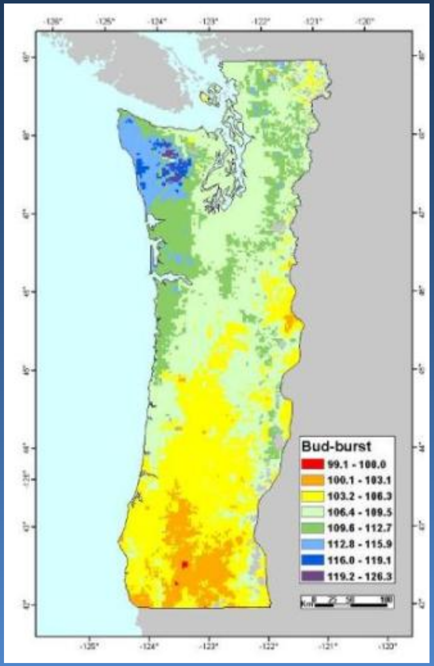
r = 0.76
Qst = 0.29

Biomass



r = 0.52
Qst = 0.13

Bud-burst



r = 0.60
Qst = 0.21

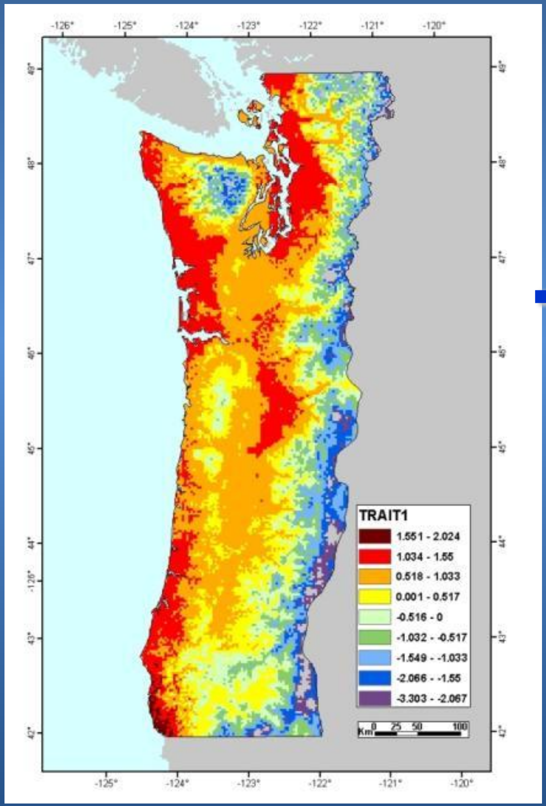
1. Populations differ
2. Traits are correlated with source environments
3. Relationships make sense

Different traits show different patterns and scales of adaptation

Seed zones derived from genecology studies

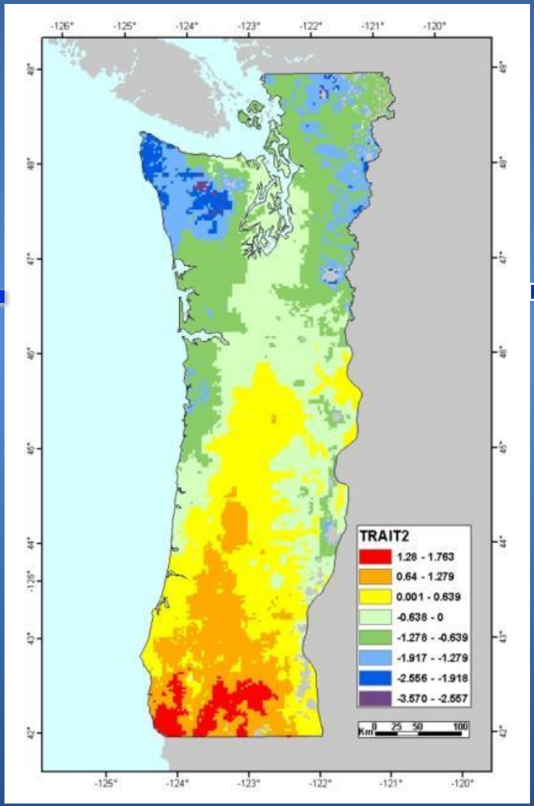
Overlay two component traits

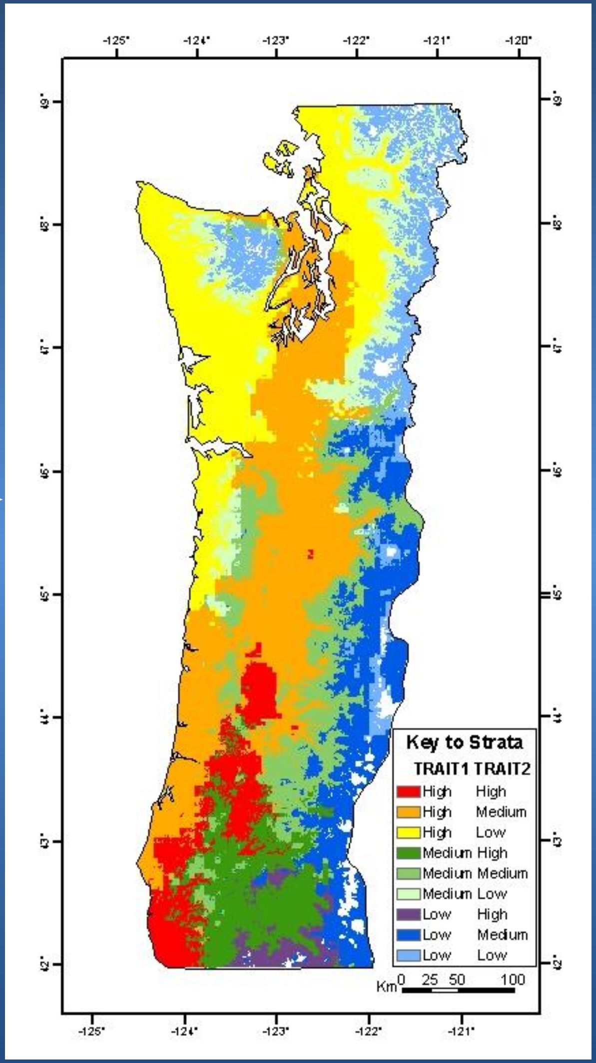
Canonical variate 1
“vigor”



+

Canonical variate 2
bud-burst, ht:diam





Advantages/disadvantages of genecology approach

- May be done in a short timeframe
- Greatly minimizes environmental variation
- Can sample many source locations from a wide range of environments
- Can produce maps of adaptive traits/climates for easy visualization and manipulation

But,

- Assumes we have measured all the most important adaptive traits
- May be difficult to synthesize results of many traits
- Assumes local is best
- Not a direct test of adaptation

Reciprocal Transplant Studies

- Populations from a range of source environments are evaluated in the same or similar range of test environments
- Provenance tests
- Can generate models to predict adaptedness as function of:
  - Planting environments (response function)
  - Source environments (genecology function)
  - Difference between planting and source environments (transfer function)
  - Both the planting environment and source environment together (universal response function)

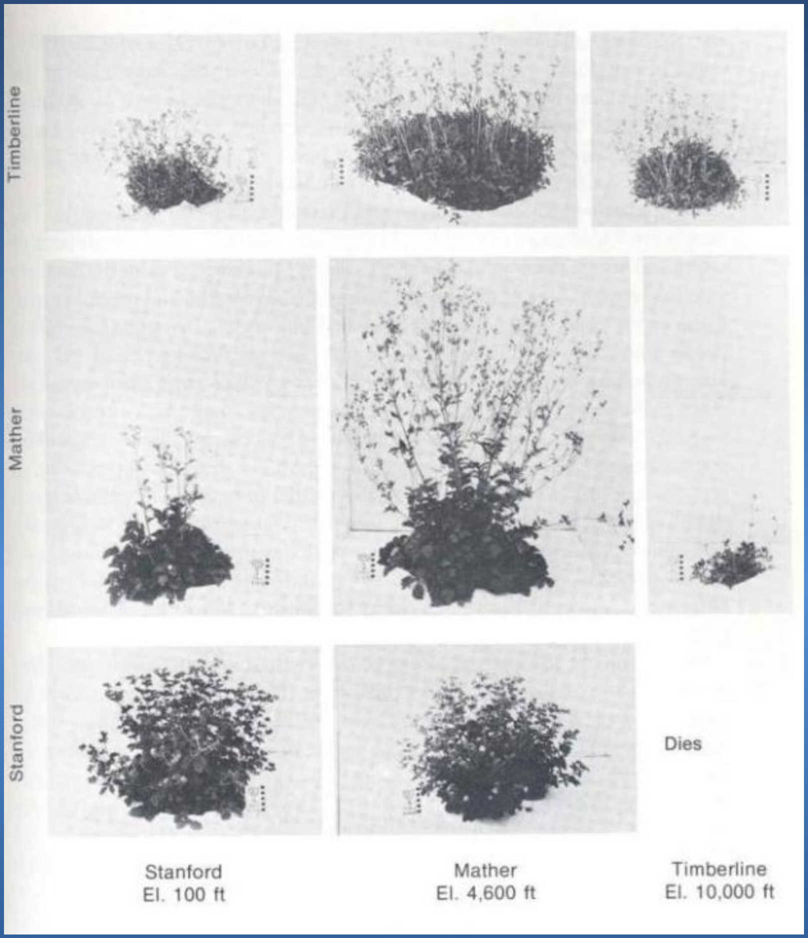
Classical studies of Clausen, Keck & Hiesey

Native to

Timberline
El. 3,030 m

Mather
El. 1,400 m

Stanford
El. 35 m



Stanford
El. 35 m

Mather
El. 1,400 m

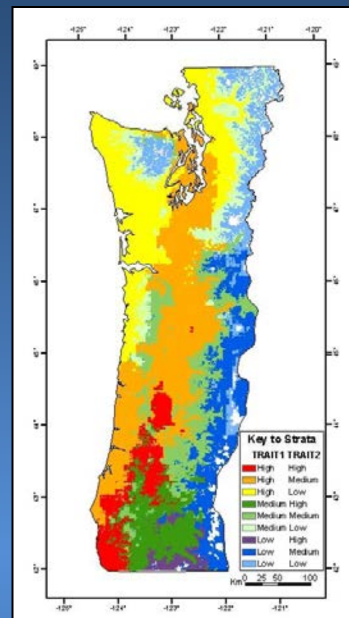
Timberline
El. 3,030 m

Grown at

Potentilla glandulosa from three different elevations planted at three different elevations (Clausen, Keck & Hiesey 1940)

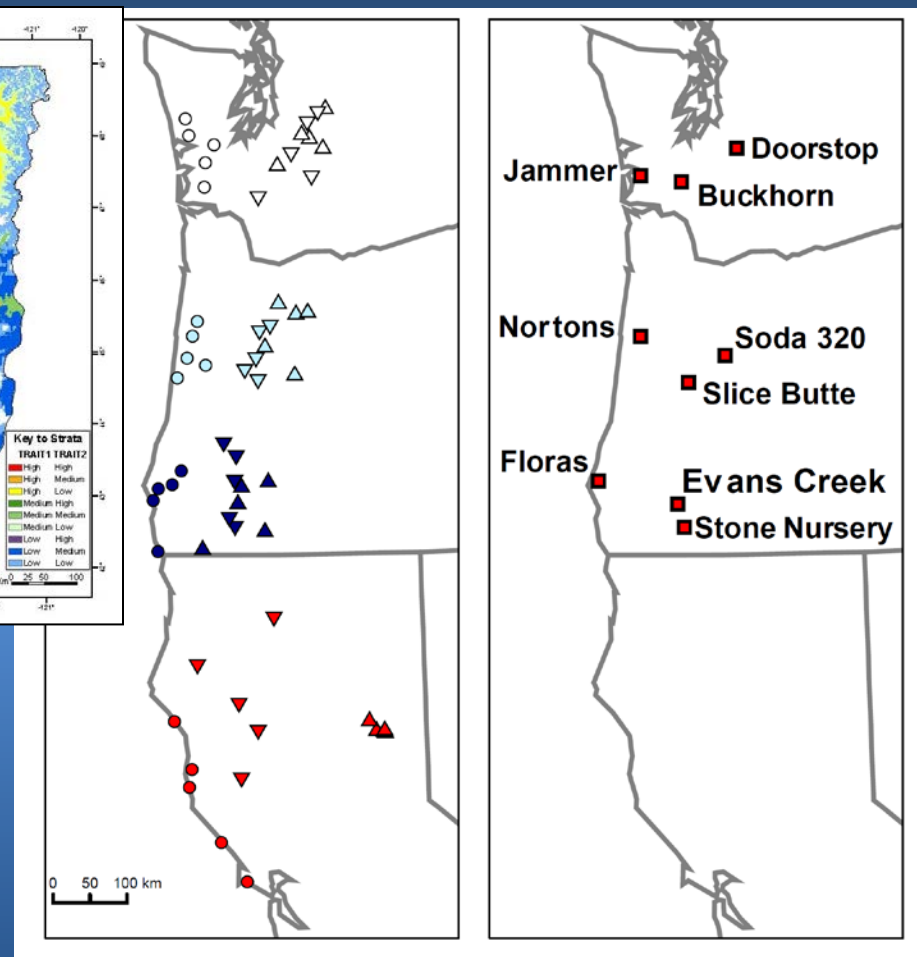
Douglas-Fir Seed Source Movement Trial

- Reciprocal transplant study
- 120 families from 60 populations from 12 diverse regions planted at sites chosen to represent 9 of those regions
- Populations chosen based on previous genecology study

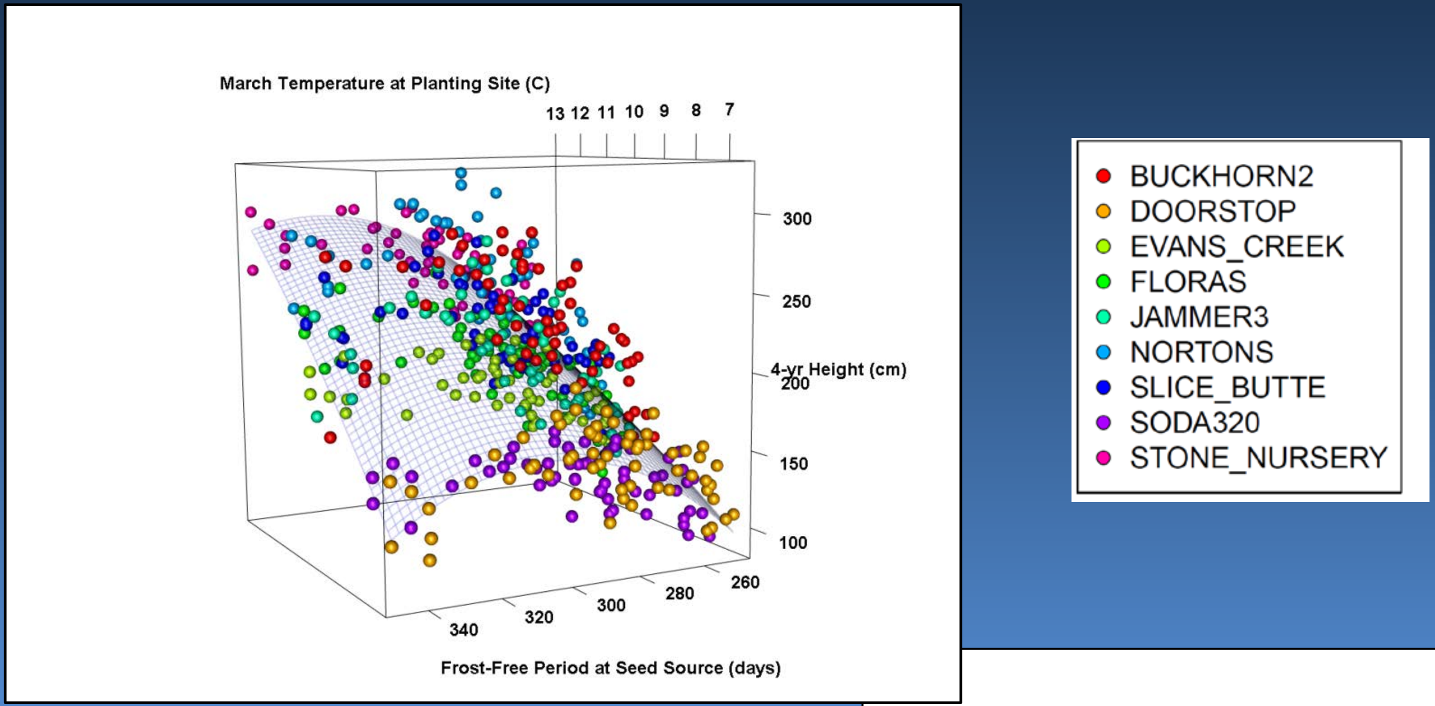


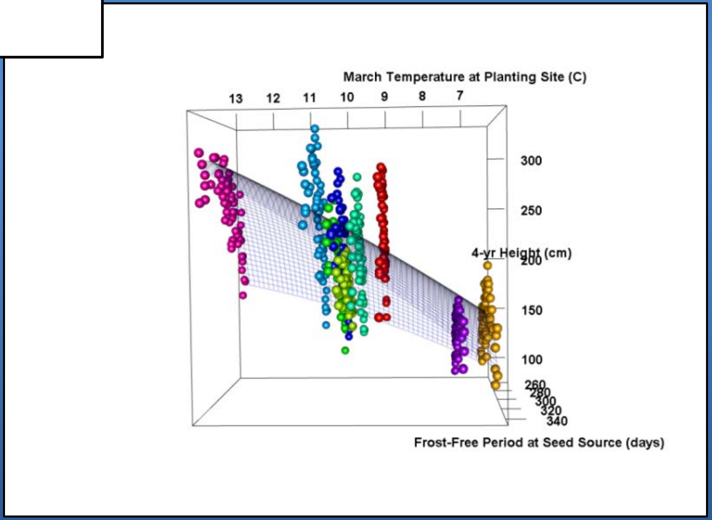
Populations

Planting Locations



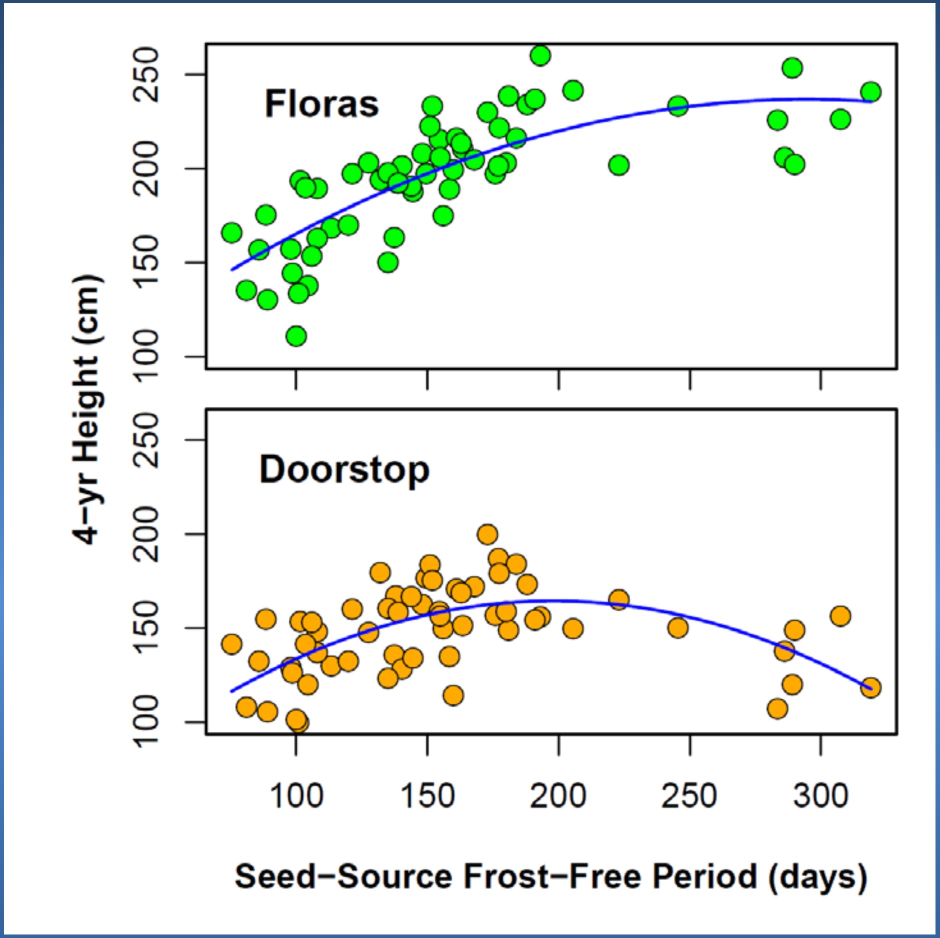
Response Surface for 4-Yr Height





- Significant differences among test sites, regions, populations within regions
- Larger differences among test sites than among populations - warmer sites have greater growth
- Significant test site x region interaction: Warmer populations have greater growth at warmer sites but not at cooler sites
- Temperature is more important than aridity

Looking more closely at two sites



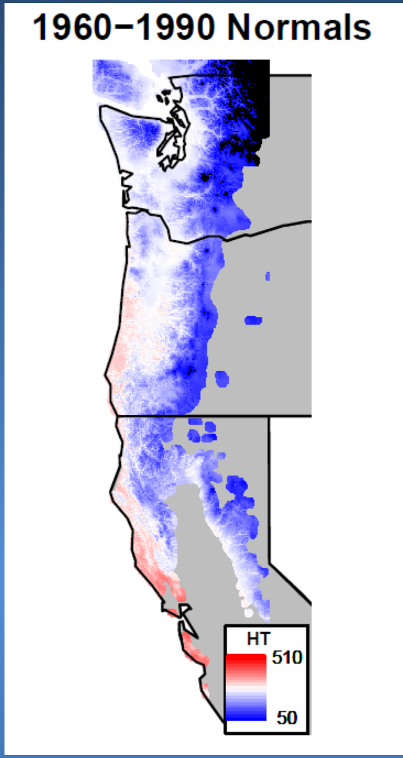
- Floras – warm site

  Frost free days = 308
- Doorstop – cool site

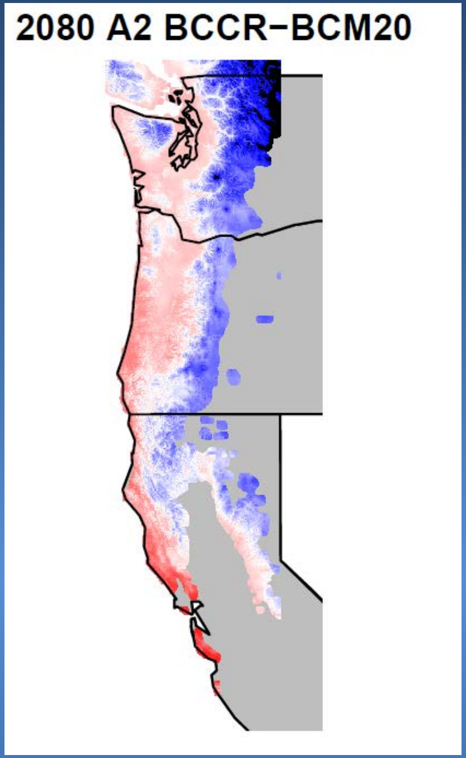
  Frost free days = 190
- Sources from similar climates are growing best at each site

Modeling Growth Given Climate Change

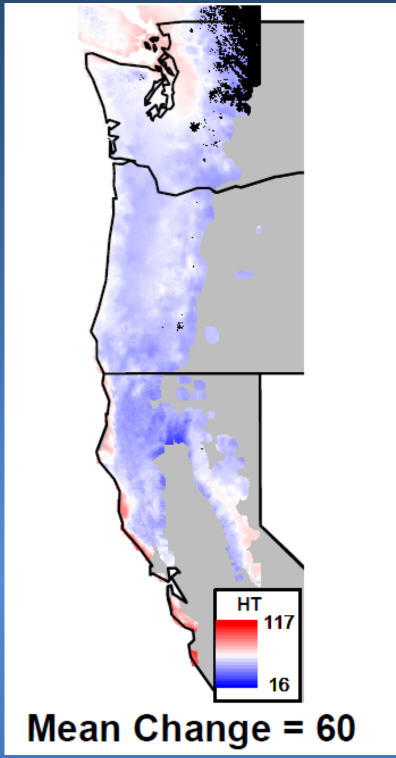
Present



Future



Difference



- Results depend on climate variables in model and future scenario
  - Using minimum temperature in March = -47 cm
- Need to also evaluate results given assumptions about using the best populations for future climates (assisted migration)

Advantages/disadvantages of reciprocal transplant studies

- Direct test of adaptation
- Can test hypothesis of local adaptation
- Can better model variables of direct interest such as stand productivity

But,

- Takes a long time for results
- Expensive to test over many planting sites and seed sources
- Few samples make it difficult to interpolate between locations to adequately model response or transfer functions, or draw maps
- Often components of adaptation are not considered, traits that might be useful for selection of populations or individuals

Some general findings

- Forest tree populations are at least moderately locally-adapted
  - Some populations show adaptive lag
- Species show different patterns and degrees of local adaptation
- Most forest trees species show significant variation for:
  - Timing of bud set and bud flush
  - Cold hardiness
  - Growth
- Traits correlate most strongly with:
  - Minimum temperatures
  - # of frost-free days
  - Drought indices
- Patterns reflect adaptation of annual growth and dormancy cycles to local temperature and drought regimes
- Provenance tests may show broader adaptation than indicated by genecology studies
  - May depend on age and rare climatic events

Distance needed to detect genetic differences in Northern Rockies (Rehfeldt 1994)

Species	Elev. (m)	Frost-free days	Evolutionary mode
Douglas-fir	200	18	Specialist
Lodgepole pine	220	20	Specialist
Engelmann spruce	370	33	Intermediate
Ponderosa pine	420	38	Intermediate
Western larch	450	40	Intermediate
Western redcedar	600	54	Generalist
Western white pine	none	90	Generalist

Point #2

Climates are changing, which affects adaptedness. Therefore, choice of species and populations matter for the future health and productivity of forest stands.

Populations are genetically adapted to historic climate

And mismatched with future climate

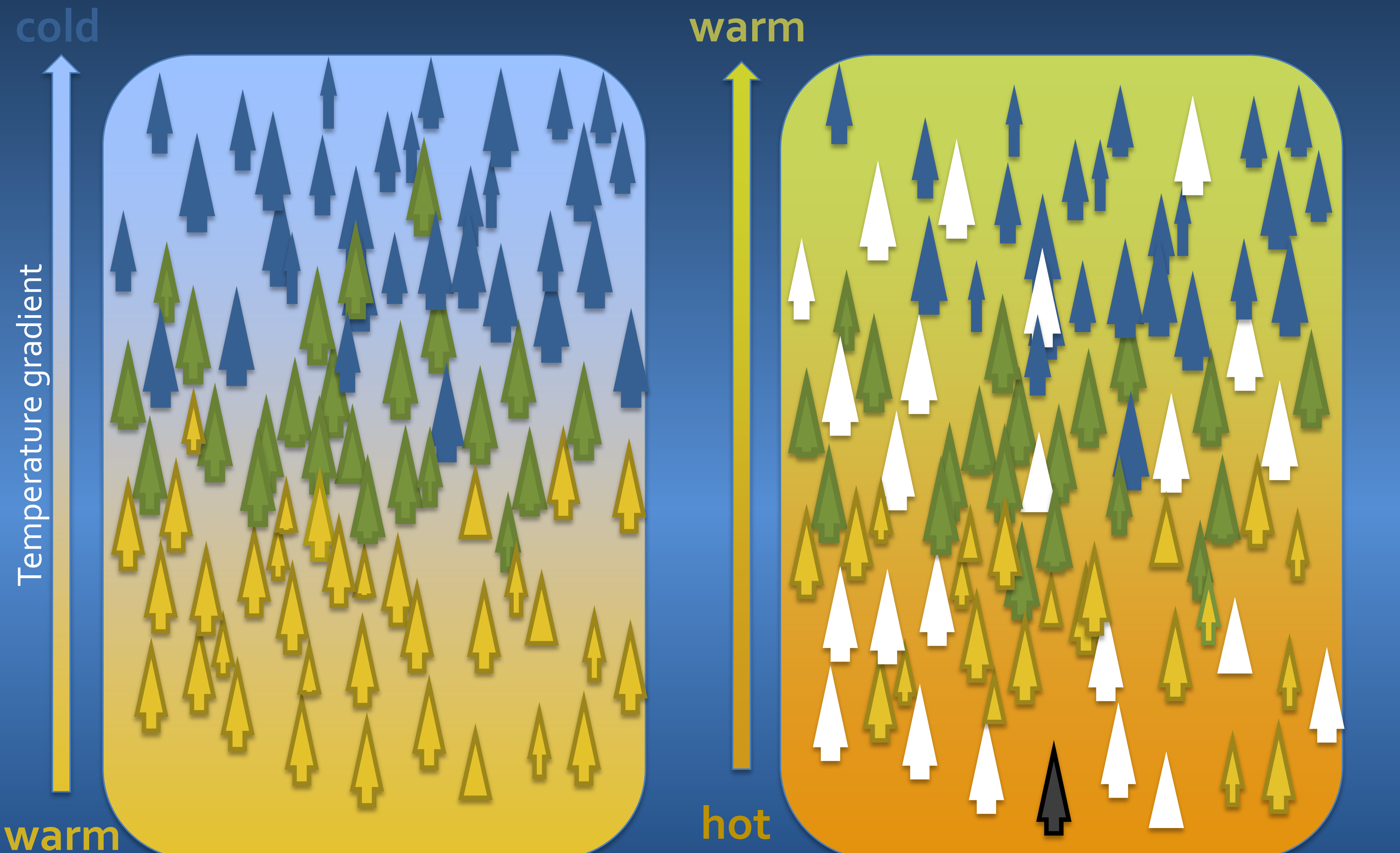
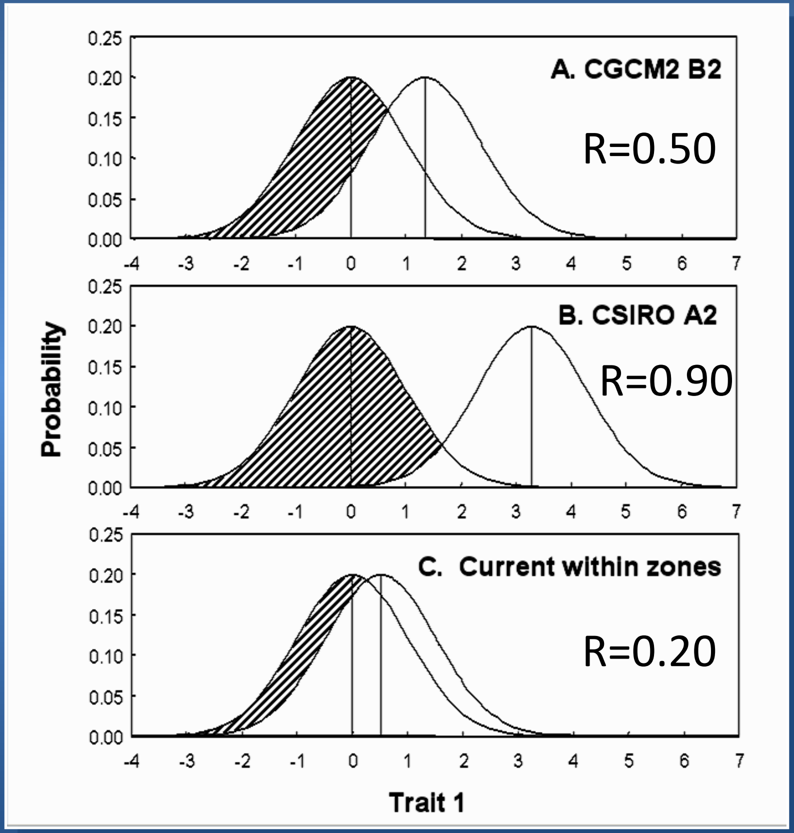


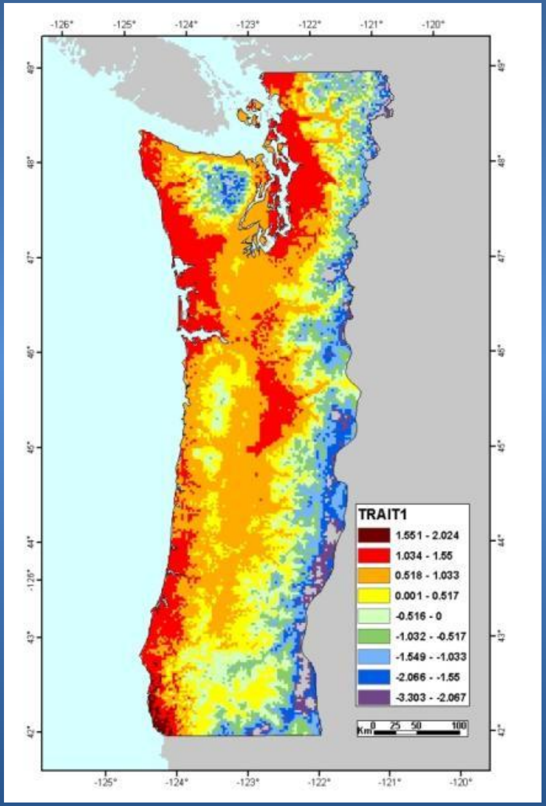
Figure courtesy of Sally Aitken, UBC

Risk of maladaptation from climate change

Risk = the mismatch between current population and the population best adapted to the changed climate (risk index proposed by Campbell 1986)

Risk = f(difference, within-population genetic variance)



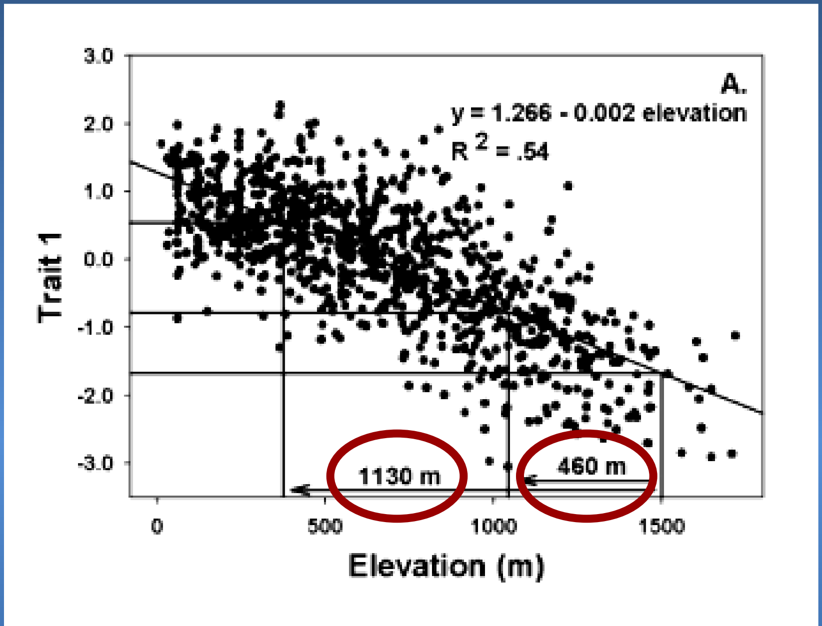


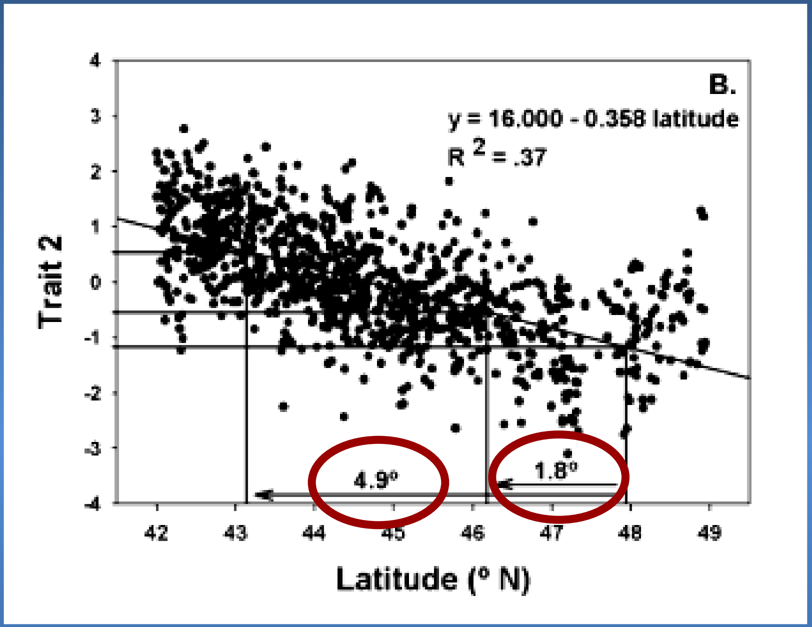
Risks of maladaptation for transfers within seed zones compared to risks of current native populations in future climates (2070-2099)

Trait	Current trait mean	Current risk in seed zones		Trait means expected to be adapted to future climates		Risk in future climates	
		Mean	Maximum	CGCM2 B2	CSIRO A2	CGCM2 B2	CSIRO A2
Trait 1	0.00	0.20	0.43	0.90	2.24	0.50	0.90
Trait 2	0.00	0.12	0.27	-0.64	-1.74	0.30	0.70
Fall cold damage	25.5	0.22	0.45	34.6	38.8	0.51	0.67
Bud-set (days)	273.6	0.15	0.32	279.3	283.6	0.36	0.59
Emergence (probits	0.0466	0.11	0.25	0.0458	0.0454	0.08	0.14
Total weight (g)	12.7	0.07	0.16	14.3	15.9	0.20	0.40
Root:shoot ratio	0.397	0.09	0.20	0.375	0.347	0.24	0.53
Bud burst (days)	106.3	0.09	0.21	105.4	103.0	0.09	0.31
Taper (mm cm^{-1})	0.188	0.14	0.29	0.184	0.187	0.12	0.10

St.Clair and Howe. 2007. Genetic maladaptation of coastal Douglas-fir seedlings to future climates. Global Change Biology 13: 1441-1454.

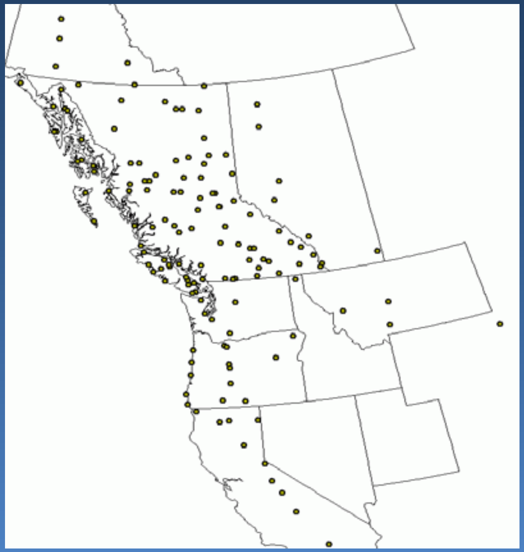
Locations of seed sources adapted to future climates



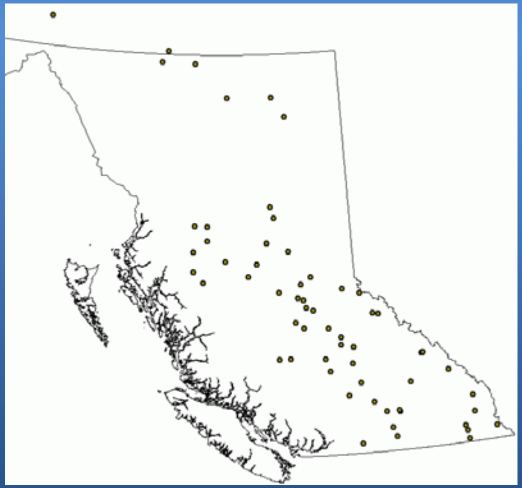


St.Clair and Howe. 2007. Genetic maladaptation of coastal Douglas-fir seedlings to future climates. Global Change Biology 13: 1441-1454.

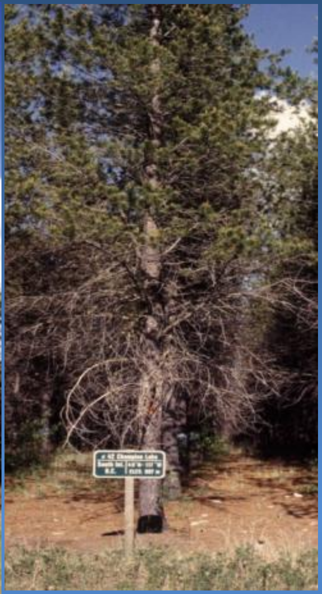
British Columbia Ministry of Forests
Lodgepole Pine Provenance Trials

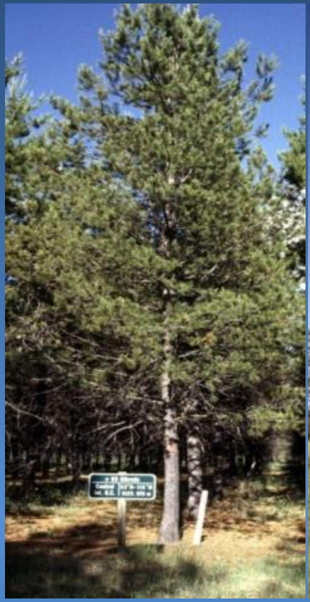


140 provenances sampled



Planted at 60 test sites





Manning	Albreda	Champion	Takhini
49 N	52 N	49 N	60 N

Variation among four populations at one test site

Using local sources, increased productivity by 7% up to 1.5 ^{o} C (2030), but decreased productivity above 2^{o}C.

Using optimal seed sources can increase productivity by 10 to 35% in future climates.

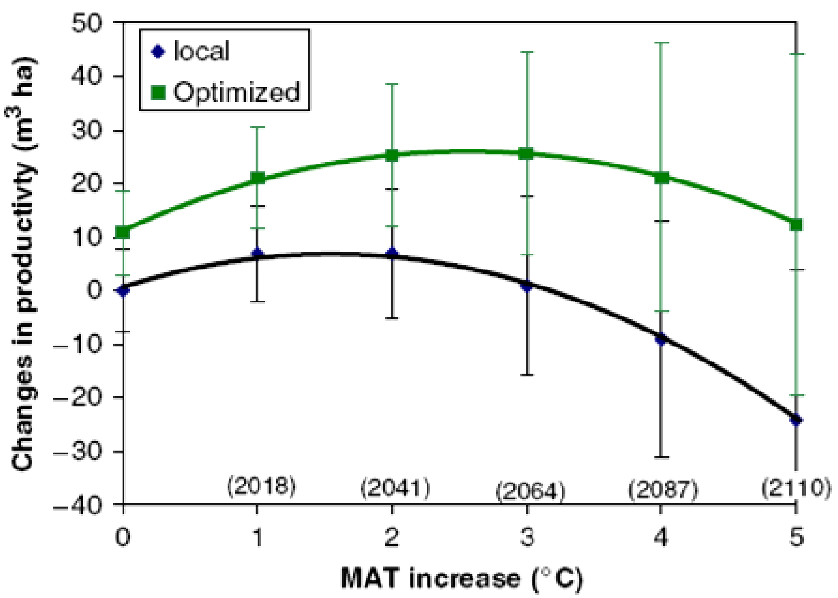
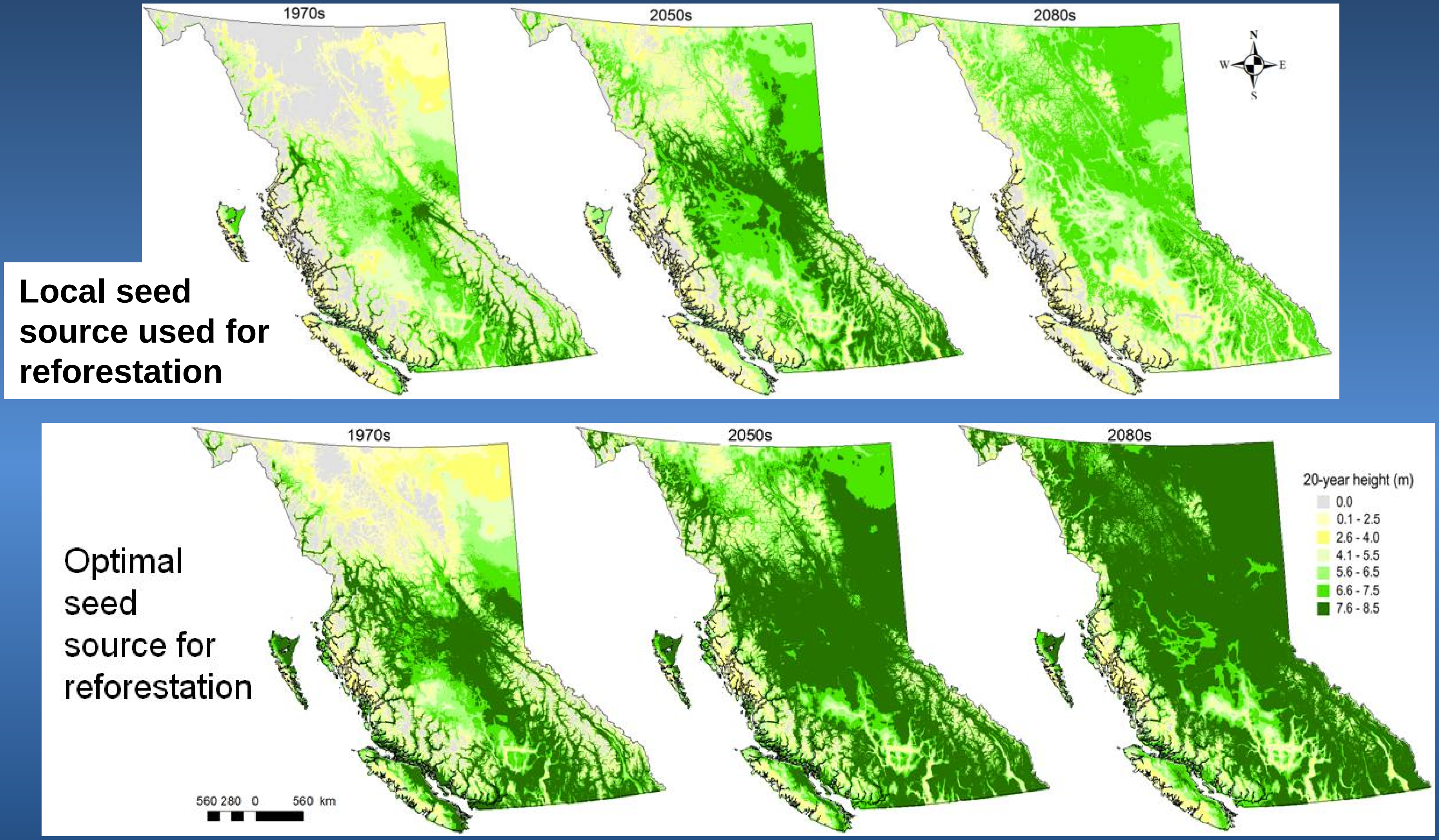


Fig. 8 Predicted changes in productivity of lodgepole pine across all seed planning units in BC for local seed vs. most productive seed source for future climates. Each increase of 1 °C in mean annual temperature (MAT) is accompanied by an increase of 1.8% increases in mean annual precipitation. Error bars indicate the 90% confidential interval for predicted means.

Wang et al. 2006. Use of response functions in selecting lodgepole pine populations for future climates. Global Change Biology 12: 2404-2416.

Lodgepole pine productivity predicted from response functions



Future climate scenario: CGCM2 A2x

Wang et al. 2010. Ecol. Appl.

Point #3

We can manage genetic variation to positively influence how plants respond and adapt to climate change.

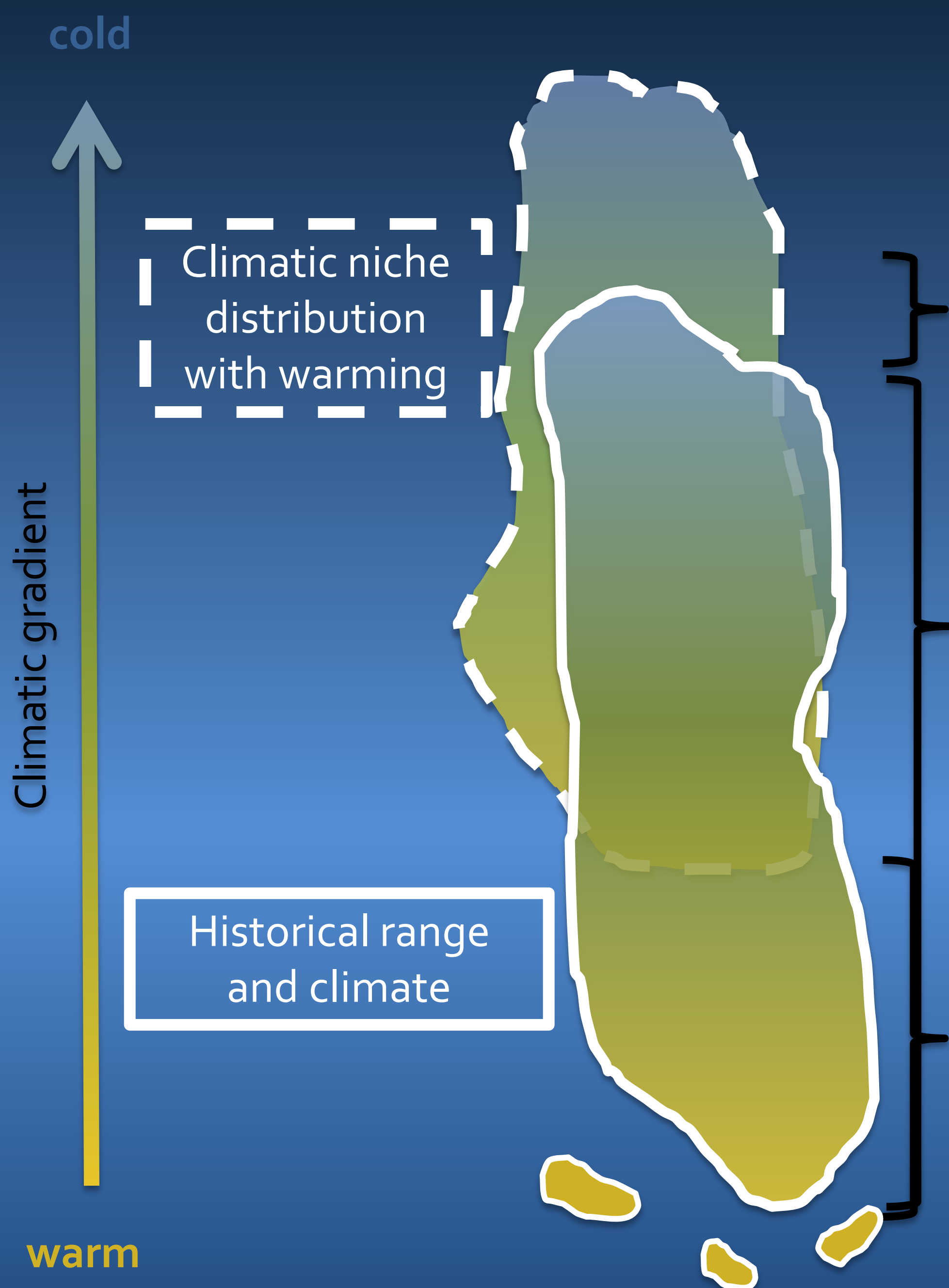
Management options for climate change:

1. Do nothing

Three possibilities:

1. Stay
2. Move
3. Decline and disappear

Natural population responses



Move:
- Natural migration from leading edge

Stay:
- Environmental change is not biologically significant
- Acclimation by individual modification (phenotypic plasticity)
- Adaptation over generations using standing variation and gene flow

Decline or disappear:
- Reductions in health and productivity
- Lagging edge population extirpation

Figure courtesy of Sally Aitken, UBC

What about phenotypic plasticity?

- Phenotypic plasticity = the ability of an individual (genotype) to change its characteristics (phenotype) in response to changes in the environment
- Phenotypic plasticity is common in plants
  - Plants modify their phenology, physiology and growth in response to changes in environments
    - Bud-set
    - Bud-burst
    - Flowering
    - Acclimation to drought
    - Growth

- However, patterns of genetic variation in adaptive characteristics associated with environmental variation suggest that phenotypic plasticity is insufficient
  - No single phenotypically plastic genotype is optimal in all environments

What is the potential for adaptation via natural selection?

Important factors include:

- Generation turnover
- Fecundity
- Intensity of selection
- Genetic/phenotypic variation
- Heritabilities

- Levels of gene flow
- Population size
- Structure of genetic variation/ steepness of clines
- Central vs peripheral populations
- Trailing edge vs leading edge

What is the potential for migration?

- Estimates of past migration rates vary
  - Davis and Shaw 2001: 200-400 m per yr
  - Aitken et al. 2008: 100-200 m per yr
  - Gugger et al. 2010 (Doug-fir): 50-220 m per yr
- But current rates of climate change require 3000-5000 m per yr

Management options for climate change:

1. Do nothing
2. Use silvicultural measures to ensure resiliency and resist change

Silvicultural options include:

- Density management
- Fuels management
- Pest management
- Reforestation/restoration

But, silvicultural options may just delay the inevitable as aging stands become increasingly maladapted.

Management options for climate change:

1. Do nothing
2. Use silvicultural measures to ensure resiliency and resist change
3. Promote natural migration and gene flow

Avoid fragmentation and maintain corridors for gene flow

But,

- Seed migration may not be sufficient
- Pollen flow may be limited by temperature-associated flowering phenology

Management options for climate change:

1. Do nothing
2. Use silvicultural measures to ensure resiliency and resist change
3. Promote natural migration and gene flow
4. Select and breed for adaptive traits within species/populations

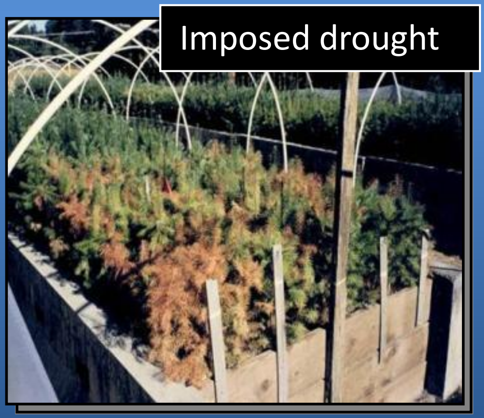
Selection and breeding

Breed for resistance or tolerance to pests

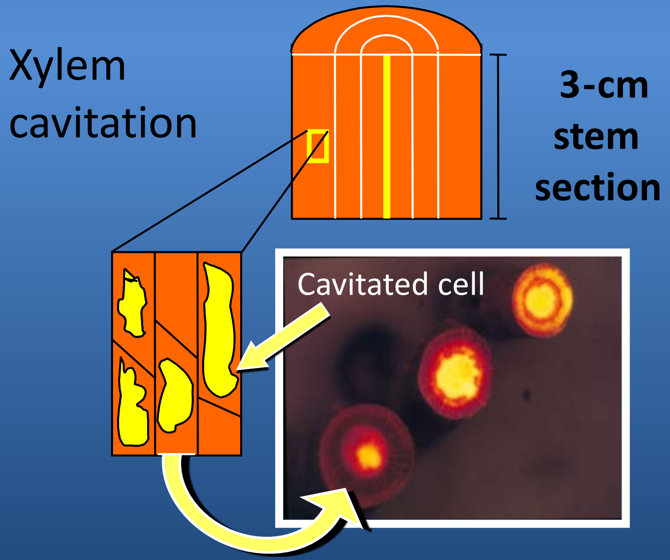
- A long-term, expensive, difficult prospect.
- Key pests are being addressed – which others will become problematic?

Breed for drought hardiness and growth phenology

- Tests have been developed to assess cold and drought hardiness.
- But breeding per se may not be needed – rely on assisted migration instead?

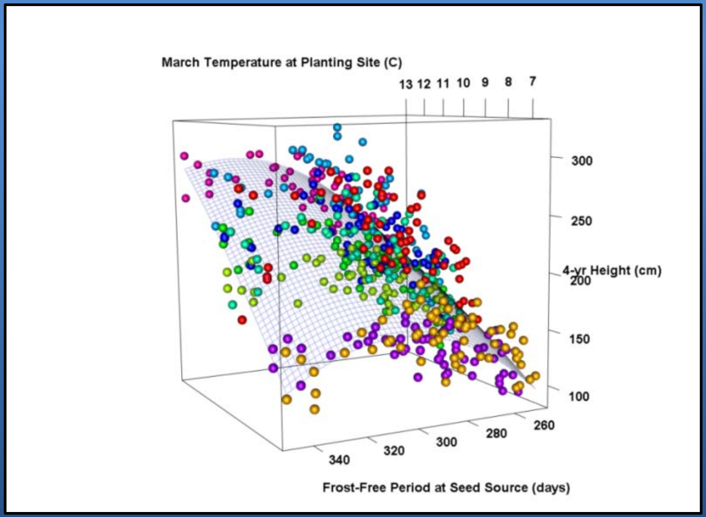


Testing for drought hardiness

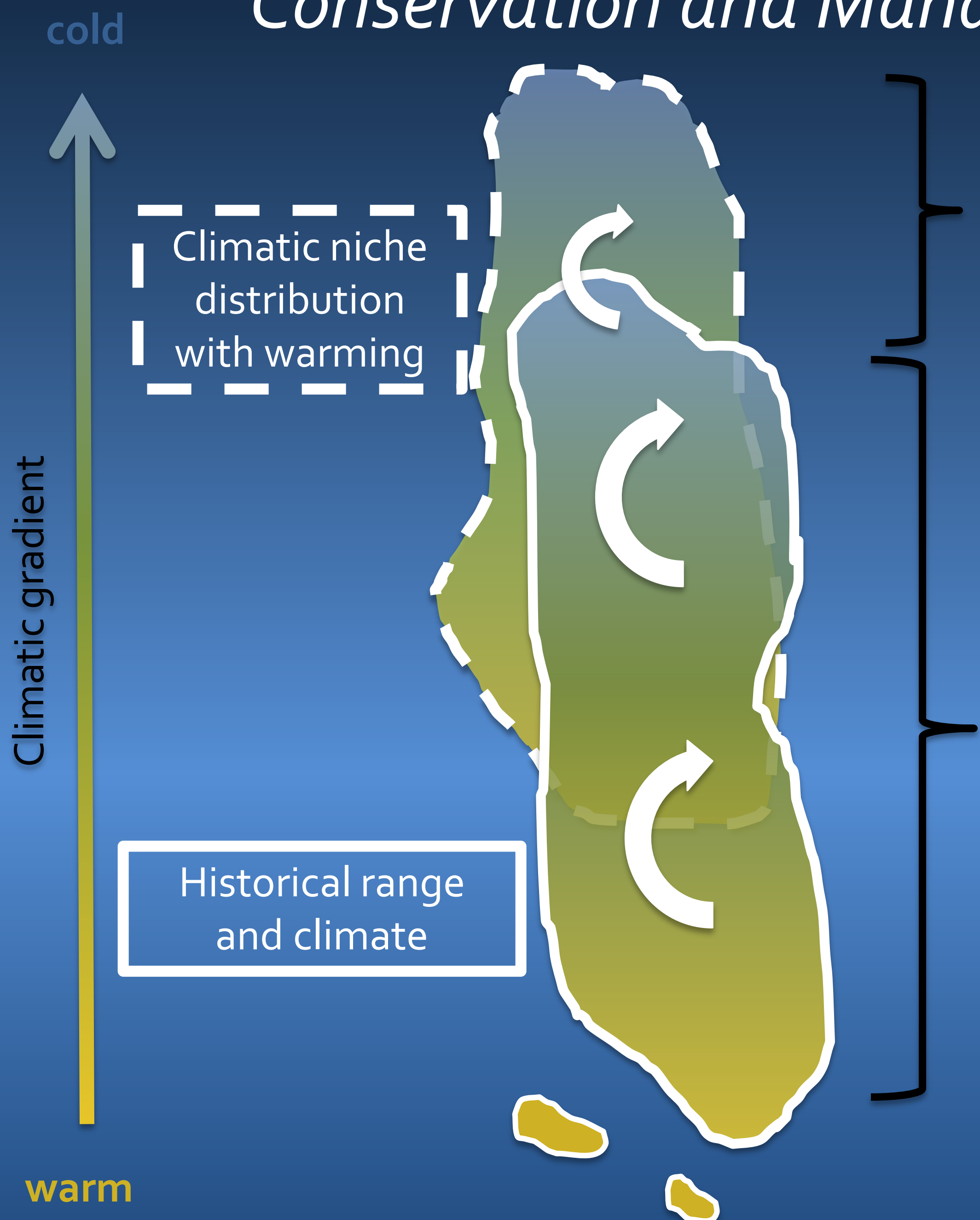


Management options for climate change:

1. Do nothing
2. Use silvicultural measures to ensure resiliency and resist change
3. Promote natural migration and gene flow
4. Select and breed for adaptive traits within species/populations
5. Gradually change species and seed sources for reforestation or restoration in anticipation of warming or in response to problems (assisted migration)



Conservation and Management Options



Long-distance introduction of exotics

Assisted colonization

Types of assisted migration

Assisted gene flow

Aitken and Whitlock. 2013. Assisted gene flow to facilitate local adaptation to climate change. Ann. Rev. Ecol. Evol. & Syst. 44: 367-388.

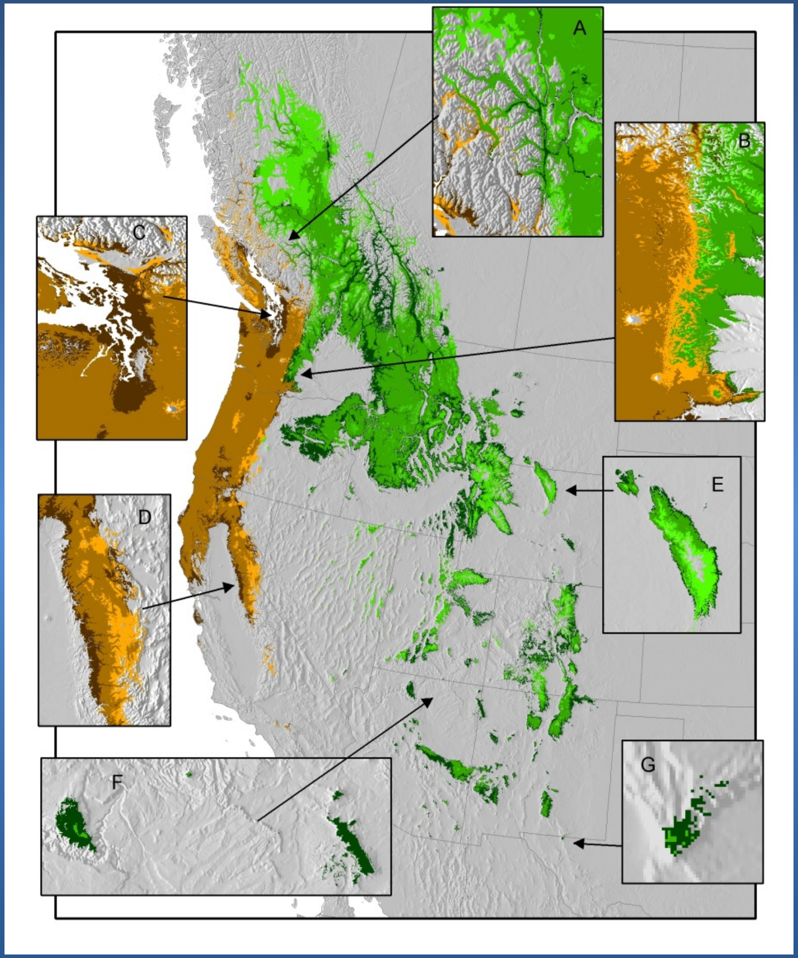
Assisted migration

Two levels to consider:

1. Species
   - Will the species survive in the changed climate?
   - Is another species more appropriate?
2. Populations

- Factors important for the realized niches of species may be different than those important for populations
  - Species: aridity, biological interactions
  - Population variation: cold temperatures, aridity

Species Level:
Realized climatic niches by 2060 for *Pseudotsuga menziesii* varieties

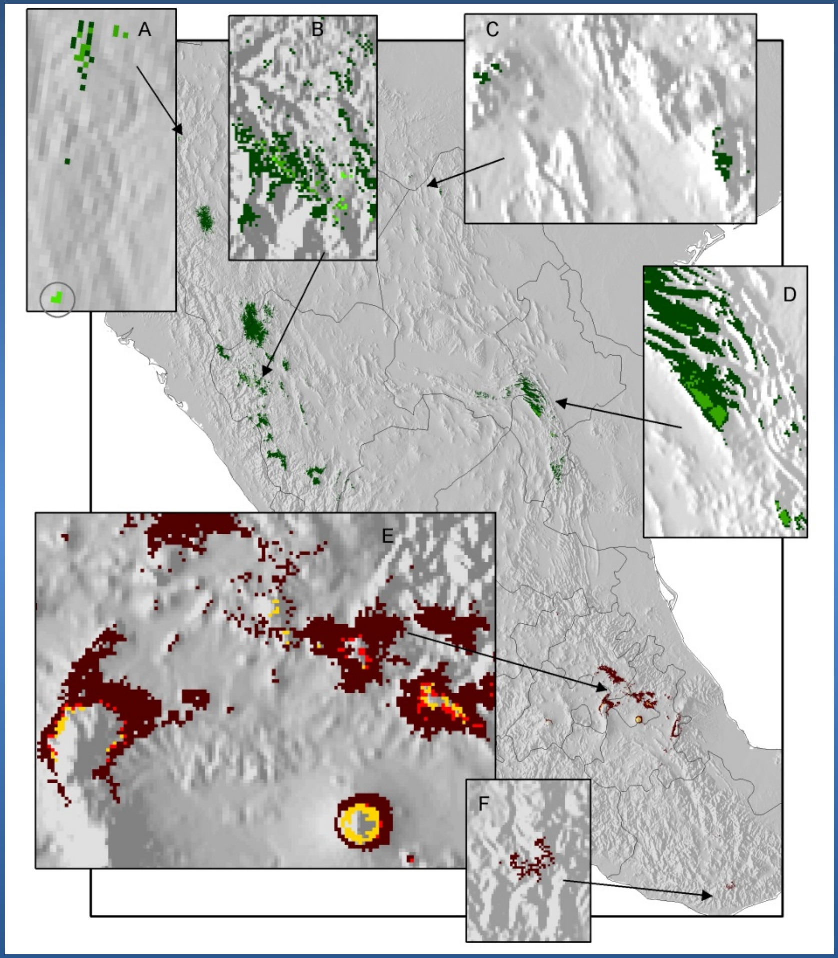


Habitat lost at the trailing edge
(lower elevations and further south)
Gained at the leading edge
(higher elevations and further north)

	Habitat lost (dark color)	**Remains suitable (middle color)**	**Habitat gained (light color)**
var. menziesii (greens)	18%	82%	18%
var. glauca (browns)	35%	65%	32%

Rehfeldt et al. 2014. Comparative genetic responses to climate for varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Realized climate niches. Forest Ecology and Management 324: 126-137.

Realized climatic niches by 2060 for *Pseudotsuga menzeiesii* in Mexico

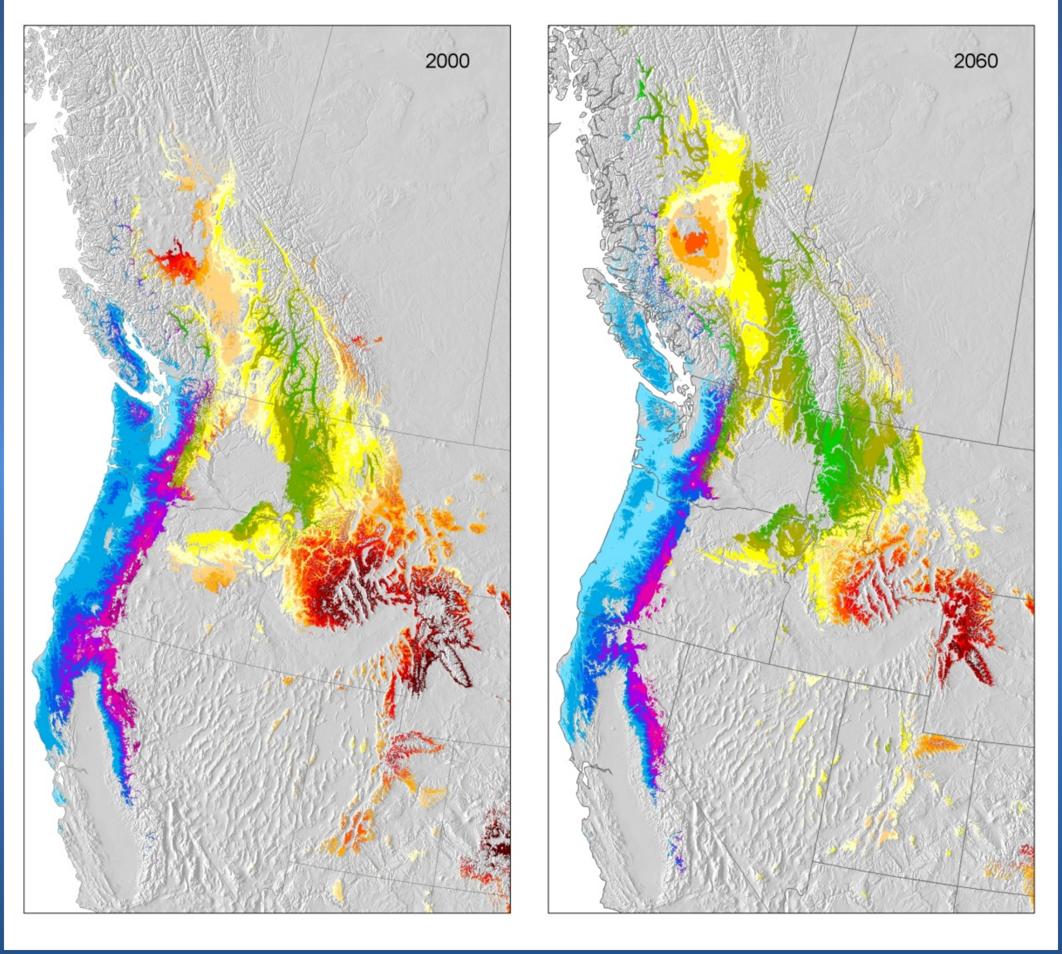


Green = var. glauca
Red = unnamed variety in southern Mexico

(only 2% suitable in future climate)

Population variation: Clines in growth potential within current and future (2060) climatic niches

Year 2000 **Year 2060**

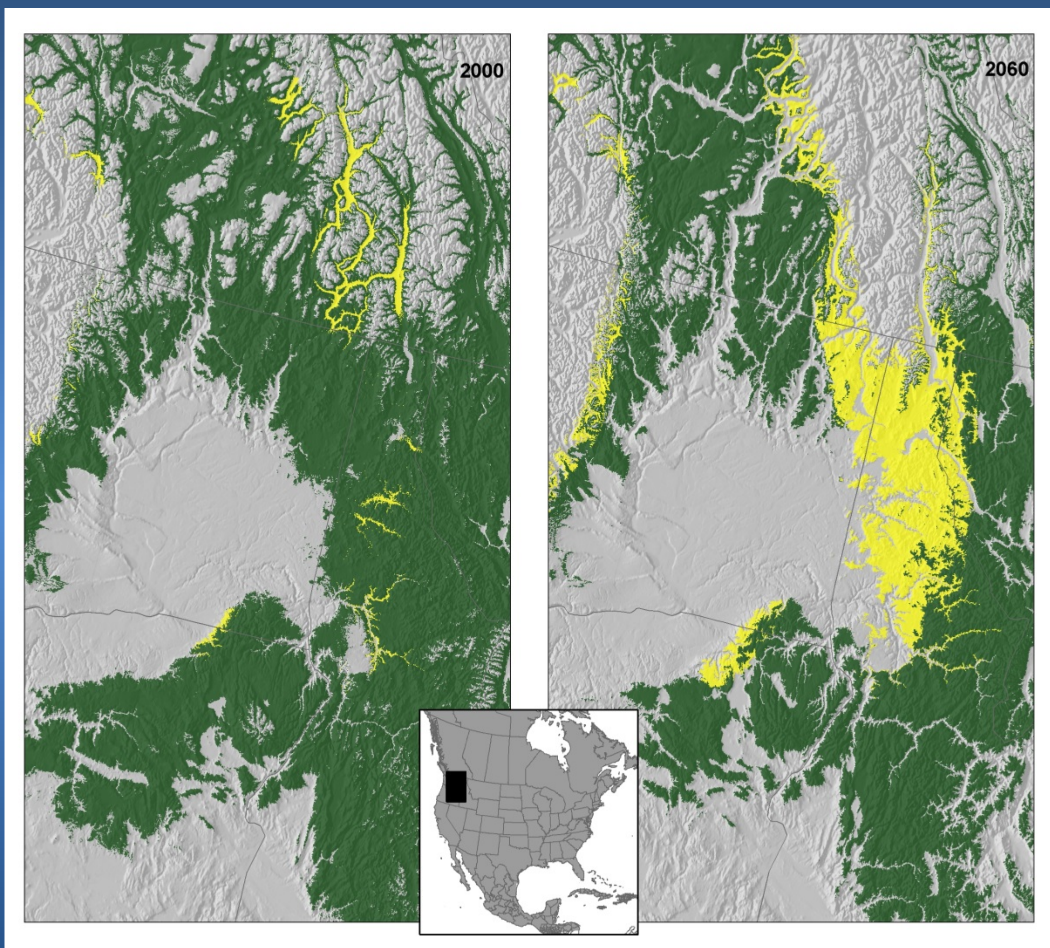


	Remaining suitable from today	**Current climatype suitable through 2060**
var. menziesii (light blue = high growth magenta = low	82%	58%
var. glauca Dark green = high Dark red = low	68%	1%

Rehfeldt et al. 2014. Comparative genetic responses to climate for varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Clines in growth potential. Forest Ecology and Management 324: 138-146.

Current seed zone for *Pseudotsuga menziesii var. glauca* in northern Idaho and southeast British Columbia and projected to 2060

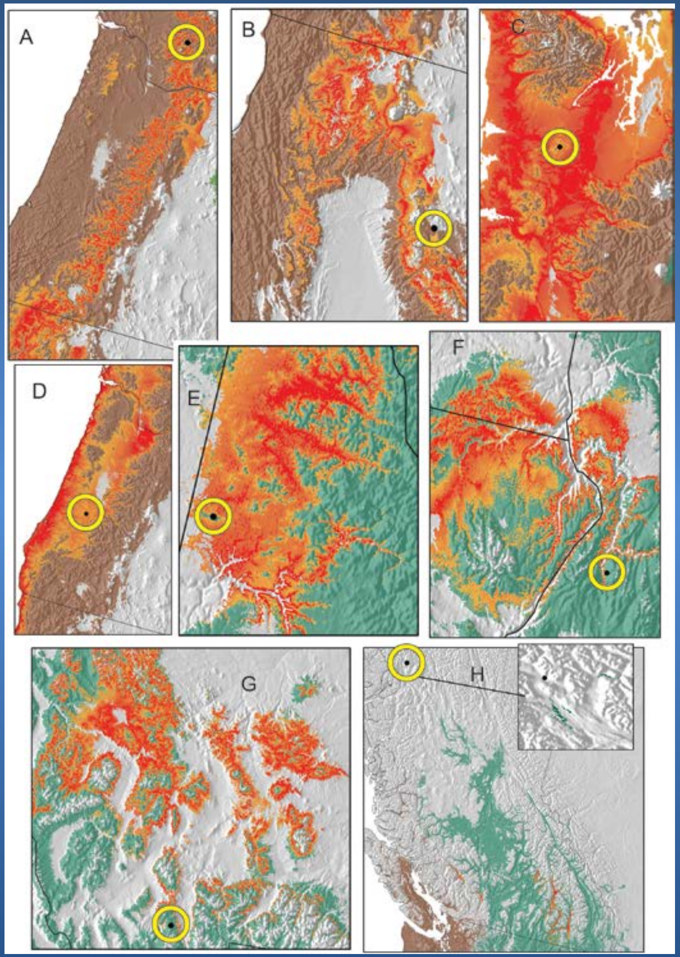
Year 2000 **Year 2060**



Yellow = current and projected seed zone
Green = current and projected species climatic niche

Rehfeldt et al. 2014. Comparative genetic responses to climate for varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Reforestation. Forest Ecology and Management 324: 147-157.

Current seed sources suitable for 2060 climate at planting sites (yellow circles) for Pseudotsuga menziesii var. menziesii (panels A-D) and var. glauca (panels F-H)



Panels A-C: Seed sources are 550-775 m lower in elevation and within 50 km distance

Panel D: 140 m lower in elevation and 70 km west along coast

Panel E: 500 m lower in elevation and 30-100 km distant

Panel F: 700 m lower in elevation and 25-80 km distant

Panel G: 500 m lower and 130 km to north

Panel H: 1,000 km to southeast

Management options for climate change:

1. Do nothing
2. Use silvicultural measures to ensure resiliency and resist change
3. Promote natural migration and gene flow
4. Select and breed for adaptive traits within species/populations
5. Gradually change species and seed sources for reforestation or restoration in anticipation of warming or in response to problems (assisted migration)
6. Enhance species and genetic diversity
   - Maintain diversity within seed sources
   - Deploy species and/or provenance mixtures within sites and across landscapes
   - Allow for selection with higher planting densities, thinning
   - Establish genetic outposts for facilitating gene flow into adjacent native stands – small number may be effective

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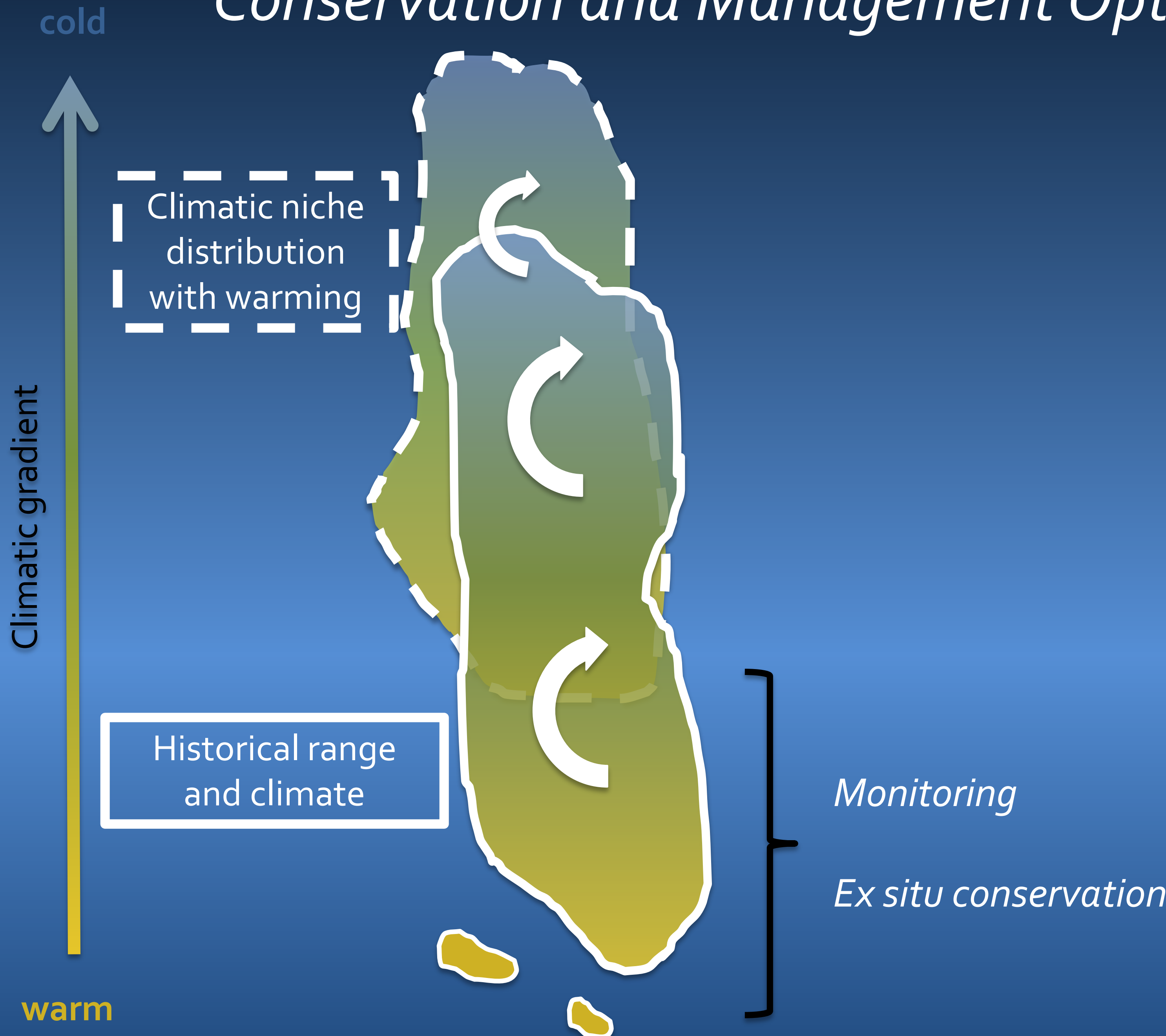
6. Enhance species and genetic diversity
7. Ensure that our genetic heritage is preserved (gene conservation)

Conservation and Management Options



Conserving genetic diversity

In situ conservation

- Locate reserves in areas of high environmental and genetic diversity
- Reduce disturbance probability and intensity
  - thinning, prescribed fire, fuels reduction, insect traps
- Supplement existing variation with genetic outposts

Ex situ conservation

- Seed collections becomes more important with increasing threats to *in situ* reserves
- Assisted migration (plantings) may also be considered a form of *ex situ* conservation

Priorities for gene conservation

- Long-lived species
- Genetic specialists
- Species or populations with low dispersal potential
- Species or populations with low genetic variation
  - Inbreeding species
  - Small populations
- Fragmented, disjunct populations
- Populations at the trailing edge of climate change
- Species or populations with “nowhere to go”
- Rare or endemic species
- Populations threatened from habitat loss, fire, disease, insects
- High economic or social value

Personal thoughts and recommendations

- Decisions now may have long-term implications.
- Most critical phase is stand establishment; although climate is a moving target, chose sources adapted to climates of the next 20 yrs.
- Large moves are not necessary; move to planting sites that are 2°C cooler than present; within current seed movement guidelines.
- Use mixtures of seed sources to account for uncertainty and climate change over the life of a stand.
- Seed zones and seed movement guidelines should be based on climate rather than geography.
- Seed collections should be bulked over a smaller climatic range than current seed zones.
- Research is important, but lack of knowledge is not an excuse for inaction.


Questions?