

Part III – Ring Width Indices: Answers

1. Are there any confusing aspects to the figures or caption above?

Yes. Several aspects of the figures could be confusing.

First, **each line represents an individual tree**, rather than an average for the entire site. Therefore, there is substantial variation among individual trees, making the overall pattern somewhat difficult to see.

Second, the two sites are quite different. **RH (Rock Harbor) contains trees that exceeded 3 m in height**, meaning that these trees eventually grew above the approximate maximum browsing height of moose. In contrast, the **SS (Siskiwit Swamp) trees remained below 2 m**, so they remained vulnerable to browsing throughout the period shown.

Third, the sites also have different **canopy structures**. RH had a more open canopy (let's more light in), while SS was in a closed-canopy (let's less light in) hardwood forest. So there will be differences in light availability and competition for that light may affect tree growth independently of moose browsing (there seems to always be more than one thing going on).

Finally, the graph shows **ring-width indices rather than simply raw annual growth measurements**. The index allows patterns in growth to be compared over time, but the individual lines should not necessarily be interpreted as identical measurements of tree growth because the trees differed in age, size, and growing conditions.

2. The moose population peaked in the mid-1970s and then declined over the next decade. How did the trees at each site respond in the years following the peak? Are the results for these samples surprising given the larger data sets for tree ring-width on the previous page?

The two sites show **very different responses** following the mid-1970s moose population peak.

At **RH (Figure A)**, tree growth increased dramatically beginning in the late 1970s and especially during the 1980s. Several trees show a substantial increase in ring width, indicating increased growth after the moose population declined. This pattern is consistent with a **release from herbivory**: fewer moose would mean less browsing on balsam fir, allowing trees to devote more resources to growth.

At **SS (Figure B)**, there is no comparable increase. Ring-width indices generally remain relatively low throughout the late 1970s and 1980s. These trees were shorter than 2 m and were located in a heavily browsed, closed-canopy forest. Consequently, they continued to experience both **moose browsing and competition for light**.

These results are not necessarily surprising when compared with the larger tree-ring data sets. The larger data sets may reveal an overall relationship between moose abundance and fir growth, but Figure 2 demonstrates that **local environmental conditions can strongly modify that relationship**. A tree's height, canopy environment, and exposure to browsing all influence whether a decline in moose abundance produces a measurable increase in growth.

3. How should the difference in canopy cover affect growth rates? How will the height of the trees at each site affect their response to changes in primary productivity? The authors suggest that primary productivity was increasing during the late 1970s and most of the 1980s—does either ring-width index appear to reflect that change?

Canopy cover should have a major effect on growth. The **open-canopy conditions at RH allow substantially more sunlight to reach the balsam firs**, increasing photosynthetic potential and therefore the amount of carbon available for growth. The closed-canopy conditions at SS restrict light availability, creating stronger competition between the firs and larger hardwood trees.

Tree height is also critical because moose can browse to approximately **3 m**. The RH trees eventually exceeded this height, meaning they could escape the most intense browsing pressure. Once moose populations declined, these trees would have both greater access to resources and less herbivory, creating favorable conditions for rapid growth.

The SS trees, however, remained below 2 m. Even if primary productivity increased, these trees remained within the browsing range of moose. Furthermore, they were growing beneath a closed canopy, so increased regional productivity would not necessarily translate into substantially greater growth for these individual trees.

Figure A does appear to reflect some of the increase in productivity during the late 1970s and 1980s because growth increased dramatically during this period. **Figure B does not show a comparable response.** This difference suggests that increasing primary productivity alone cannot explain the growth patterns. The response at RH is more consistent with a combination of increased productivity **and release from moose herbivory.**

4. Which hypothesis do you feel is best supported by the ring-width chronologies above?

The ring-width chronologies provide stronger support for the **top-down trophic cascade hypothesis**, although they do not completely eliminate the possibility of bottom-up control.

The strongest evidence is the dramatic increase in growth at RH following the decline in moose abundance. The timing is important: **moose numbers declined, and fir growth subsequently increased.** Because these trees were capable of growing above the normal browsing height of moose, reduced browsing pressure could have allowed them to take advantage of favorable growing conditions.

The lack of a similar response at SS demonstrates that the relationship is more complicated. However, rather than disproving the trophic cascade hypothesis, it suggests that the effects of predators and herbivores are **mediated by local environmental conditions** such as canopy cover and tree height.

Therefore, the evidence favors a top-down effect, but it would be inappropriate to conclude that all variation in fir growth is caused by wolves and moose. Climate, sunlight, soil conditions, and primary productivity also contribute.

5. What final conclusions can you draw about the interactions between each trophic level on Isle Royale? Is control exerted from the top down, as suggested by the trophic cascade model, or are interactions between trophic levels ultimately controlled by primary productivity?

The evidence suggests that **both top-down and bottom-up forces operate simultaneously**, but the ring-width data provide meaningful evidence for a top-down trophic effect.

The basic interaction can be represented as:

Wolves → Moose → Balsam fir

When wolf predation increases, moose abundance and/or browsing pressure can decrease. Reduced browsing allows balsam fir to survive and grow more successfully. This is particularly apparent at RH, where trees showed a strong growth response following the decline in moose abundance.

At the same time, **primary productivity provides the energy that supports the entire food web**. Climate, precipitation, temperature, sunlight, and nutrient availability influence plant productivity and therefore affect the resources available to herbivores and predators. The fact that the two fir populations respond differently demonstrates that environmental productivity and habitat characteristics can modify the strength of trophic interactions.

Therefore, I would not describe Isle Royale as being controlled exclusively from either the top down or the bottom up. A better conclusion is that **top-down trophic interactions occur within a bottom-up environmental framework**. Primary productivity establishes the conditions under which the food web operates, while wolves and moose can strongly influence how that productivity is distributed among trophic levels.

This is an important distinction because it shows that ecological systems are not simple linear chains. **Predators can indirectly influence plants, but the strength of that effect depends on environmental conditions and characteristics of the plant community.**

6. Design an experiment that would allow you to clarify any ambiguities from Figures 1 or 2. Why might an experimental approach prove advantageous in this situation?

A useful experiment would manipulate **moose browsing pressure while controlling for other environmental variables**.

One possible design would be to establish multiple plots containing balsam fir across both RH and SS. Within each site, plots could be assigned to different treatments:

- **Moose exclusion:** Install fencing to prevent moose from browsing the firs.
- **Control plots:** Leave plots accessible to moose.
- **Different canopy treatments:** Include plots under closed canopy and plots with increased light availability.

- Measure **annual ring width, tree height, stem growth, survival, leaf production, and light availability** over several years.

The researchers could then compare tree growth among the treatments. If trees protected from moose show substantially greater growth than unprotected trees under otherwise similar conditions, this would provide stronger evidence that **herbivory is limiting fir growth**.

The experiment could also distinguish between the effects of **moose browsing and primary productivity**. For example, if fenced trees in both high- and low-light environments grow better than browsed trees, browsing is likely an important limiting factor. If increased light produces a strong response regardless of browsing treatment, then productivity/light availability may be more important.

An experimental approach would be advantageous because Figures 1 and 2 are primarily **observational data**. They demonstrate correlations, but correlation does not establish causation. The decline in moose abundance and increase in fir growth occurred at approximately the same time, but other factors—such as climate, precipitation, temperature, disease, or changes in forest structure—could also have contributed.

By experimentally manipulating one factor while keeping other factors as constant as possible, researchers could determine whether **reducing moose browsing actually causes increased fir growth**. Replication across multiple plots and over multiple years would make the conclusions much stronger than relying solely on naturally occurring population changes.

Overall conclusion

The most compelling interpretation of Figure 2 is that **the decline in moose browsing contributed to increased balsam fir growth at RH**, supporting a top-down trophic cascade. However, the contrasting response at SS demonstrates that trophic cascades are not uniform throughout an ecosystem. **Canopy structure, tree height, light availability, and primary productivity can determine how strongly a change at one trophic level affects another**. Thus, Isle Royale provides evidence for both top-down and bottom-up regulation, with their relative importance varying across space and environmental conditions.