

How do gall-forming social aphids keep their closed nest clean?



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Summary

Some social aphids form completely closed galls on their host plants, wherein hundreds to thousands of aphids grow and reproduce for at least a several months in isolation. So far, why the aphids in closed galls are not drowned and killed by accumulated honeydew has been an enigma. In this study, we

found a novel plant phenotype that the inner wall of the closed galls absorbed and removed honeydew via the vascular bundle system. This plant-mediated waste removal system was induced by aphids, but not by plants, due to their manipulation of gall morphology and physiology, which could be regarded as "indirect social behavior" of the social aphids.

Introduction: waste problems in aphid galls

Plant sap-sucking aphids produce sticky honeydew, which drowns and kills aphids if it accumulates in the gall.

Open galls

A gall of *Tuberaphis styraci*

Soldiers discard honeydew droplets from gall openings.

Closed galls

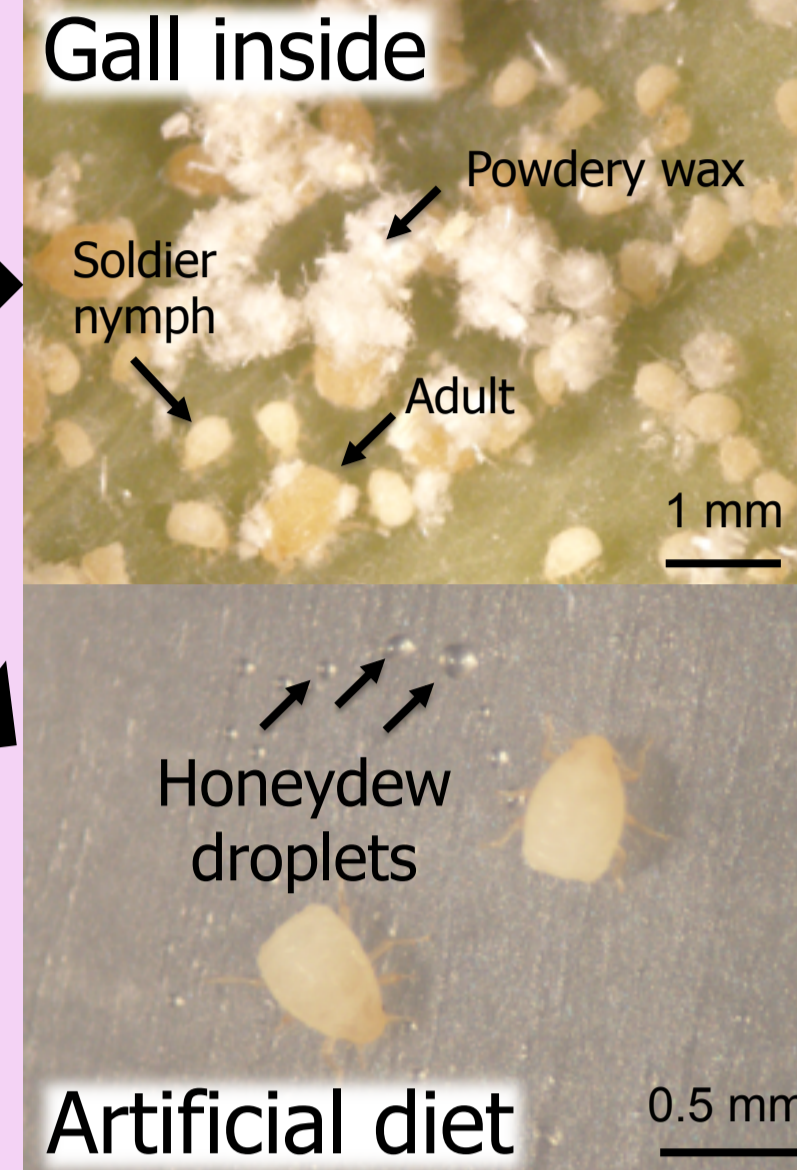
A gall of *Nipponaphis monzeni*

Soldiers can NOT remove honeydew

We observed closed galls, but surprisingly,

- No accumulation of honeydew were detected in closed galls of *N. monzeni*.
- However, *N. monzeni* aphids produced honeydew on an artificial diet system.

Hypothesis
Is the honeydew absorbed by the gall tissue?



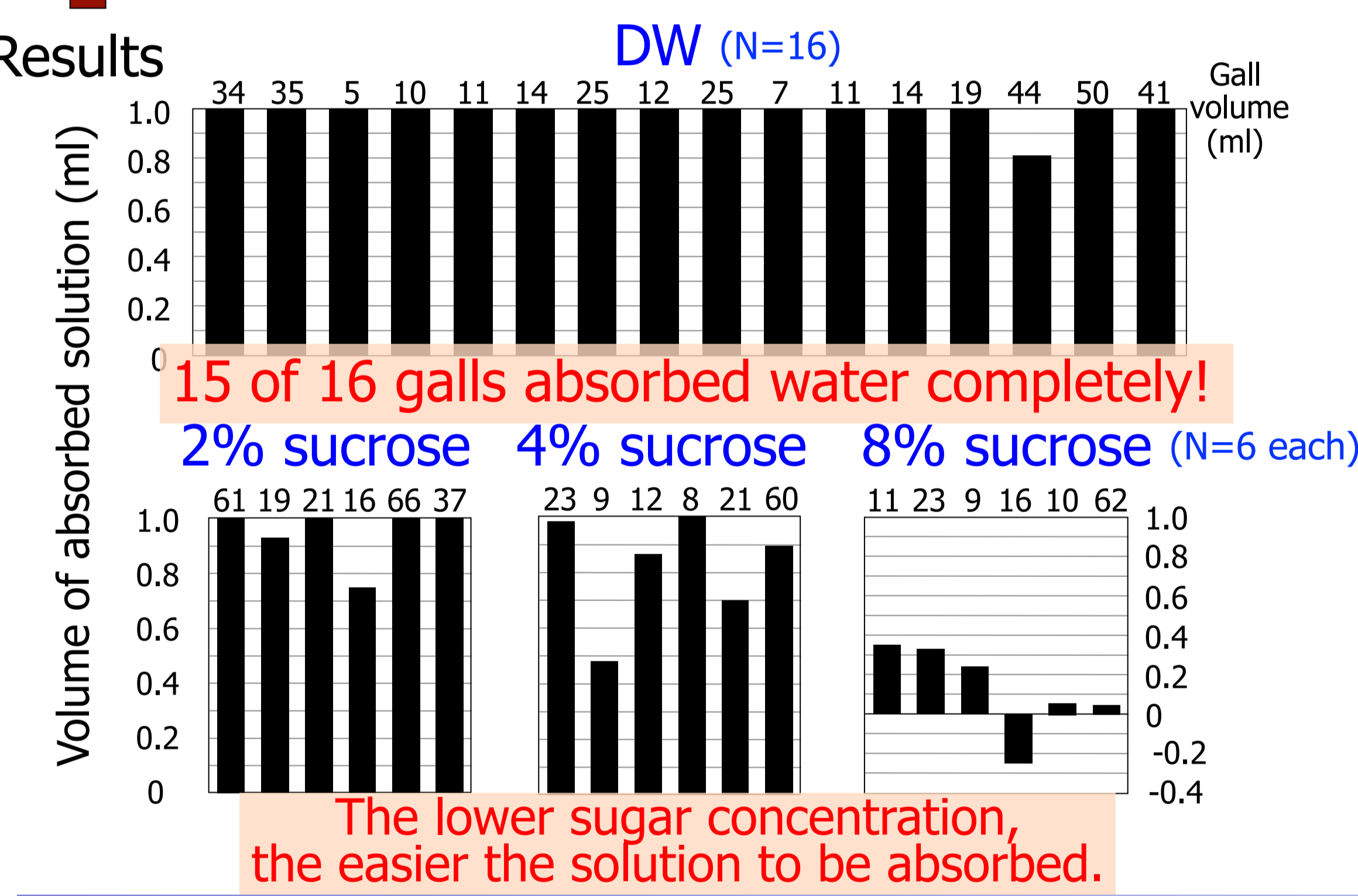
Water-absorbing property in completely closed galls of *N. monzeni*

(I) Field experiments

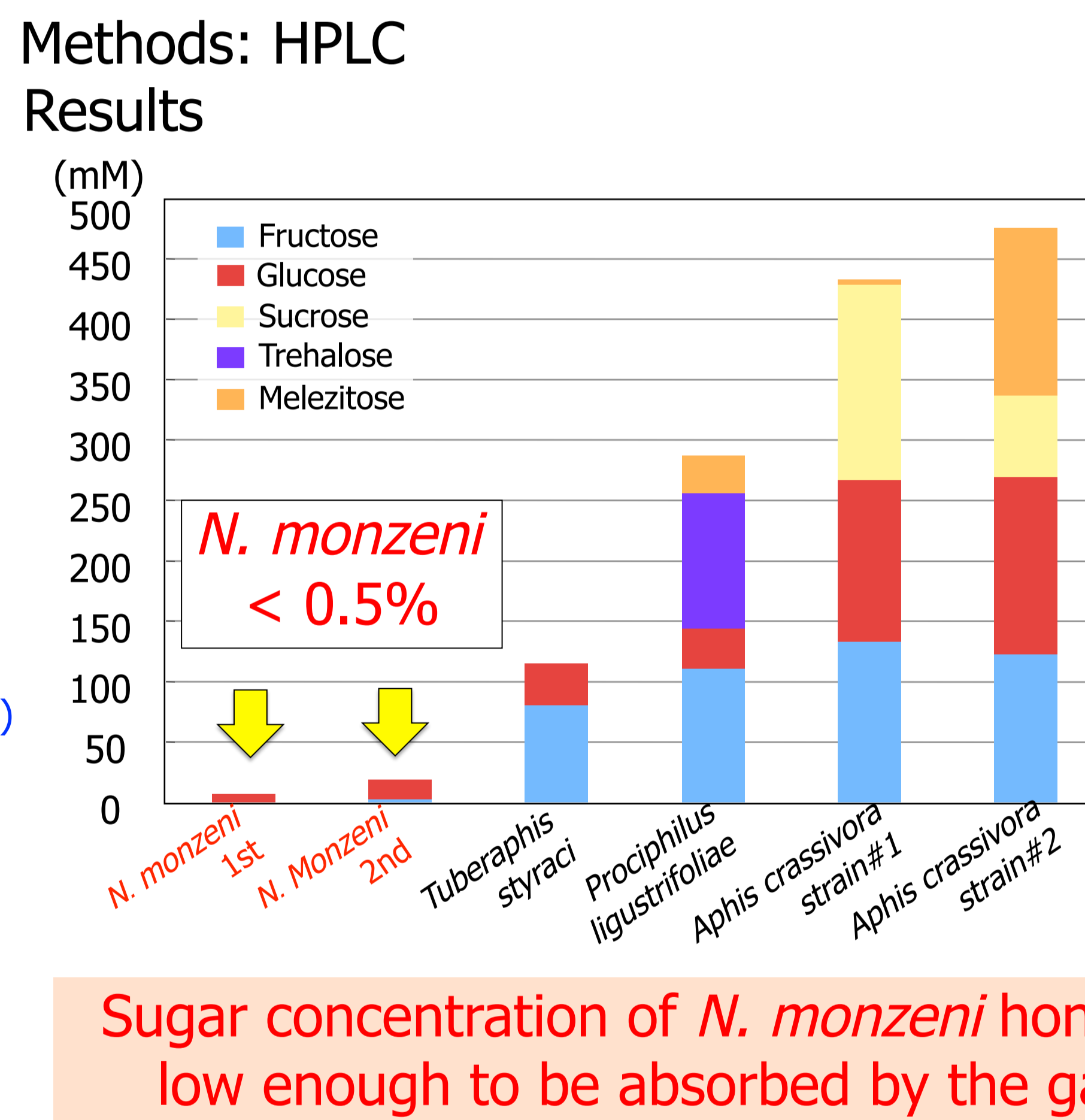
Methods

- (1) Bored a small hole
- (2) Injected 1ml of water or sucrose solution
- (3) Sealed the hole with an adhesive

Amount of the solution remained in the gall after 20 h were measured.



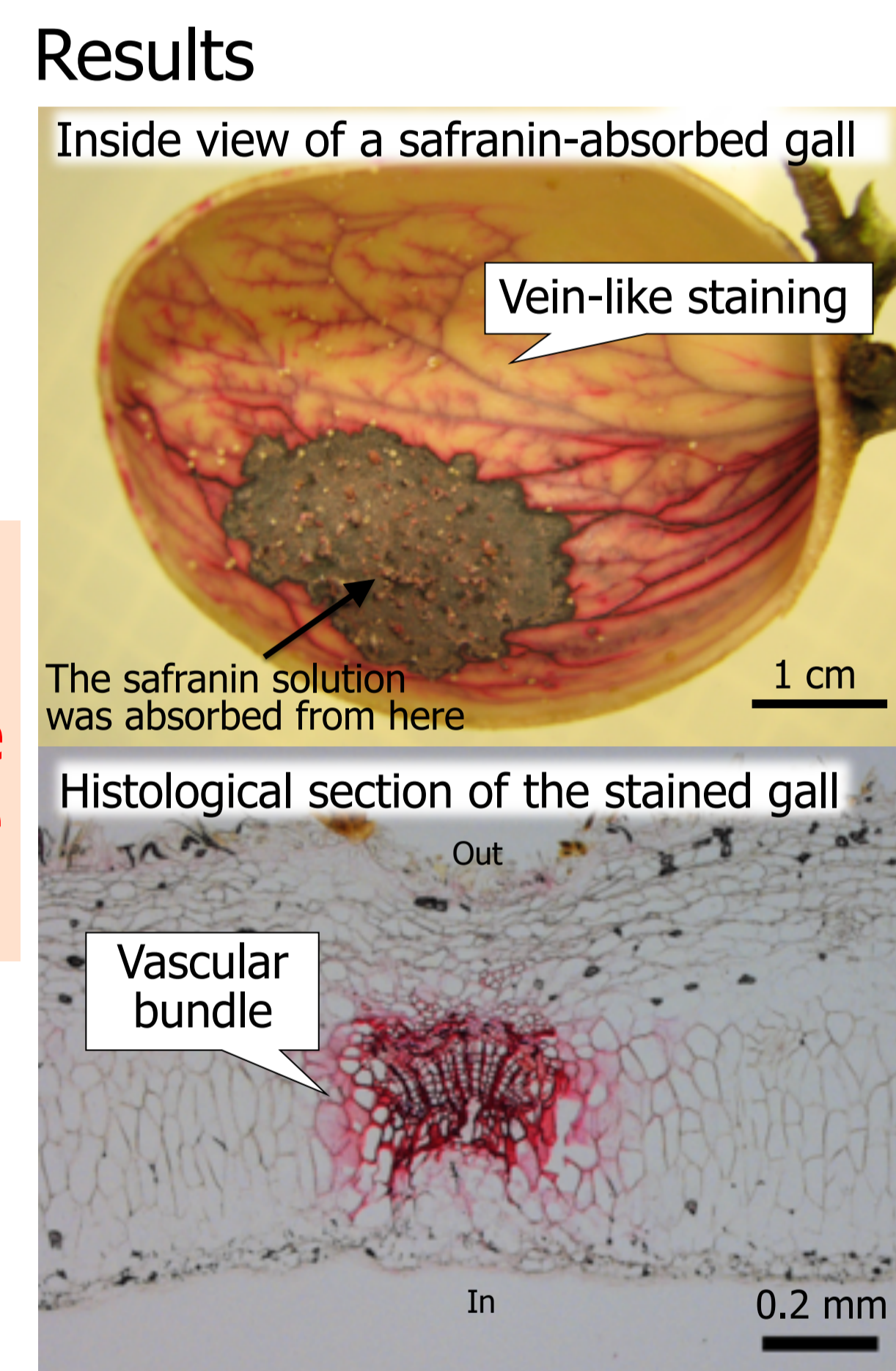
(II) Sugar analysis of aphid honeydew



(III) Where was the water transported?

Methods: Water absorption routes was stained by 0.5ml of 0.2% safranin solution for 20 h.

The absorbed water was removed by the vascular bundle system.



Why watery waste is absorbed by closed galls, but not by open galls?

Hydrophobicity and ultrastructure of inner surface of closed and open galls were examined.

Water-absorbing closed gall

Aphid: *N. monzeni*
Host plant: *Distylium racemosum*

Hydrophilic inner surface

Thin and spongy surface layer

Water-absorbing closed gall

Aphid: *Ceratovacuna nekoashi*
Host plant: *Styrax japonicus*

Hydrophilic inner surface

Thin and spongy surface layer

Water-unabsorbing open gall

Aphid: *T. styraci*
Host plant: *Styrax obassia*

Hydrophobic inner surface

Thick and distinct wax layer

Water-unabsorbing open gall

Aphid: *Ceratovacuna japonica*
Host plant: *Styrax japonicus*

Hydrophobic inner surface

Thick and distinct wax layer

Two congenic aphid galls on the same plant

Structural differences of the wax layer of the gall inner surface determined the water-absorbing property. The aphids, but not the plants, induced the water-absorbing property by manipulation of gall morphology and physiology.

Conclusion

Closed gall-forming aphids induced a plant-mediated waste removal system to reconcile colony defense and hygiene, which can be regarded as "indirect social behavior" of the social aphids.