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## PRACTICAL TOOLS

# A guide to collecting samples for flower and fruit developmental studies

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## Abstract

1. Developmental studies of flowers and fruits provide important data for evolutionary studies of flowering plants. Collecting the right samples is therefore crucial.
2. For appropriate sampling, we distinguish between early, mid and late developmental stages, followed by anthesis, fruit developmental stages and fruit maturity.
3. Sampling is preferably carried out in the field, but botanical gardens are also very important for sampling, always taking into account local regulations and legislation. Herbaria and alcohol collections in natural history institutions can also be consulted for material or stages that are difficult to obtain.
4. *Practical implications.* We provide a list of equipment and materials required for collecting and storing, including details of fixatives. Finally, we also include some useful tips on how to collect the relevant samples for developmental and comparative morphological studies.

## KEYWORDS

collecting, comparative morphology, evolution, flower development, fruit development

## 1 | WHY COLLECT?

From the earliest attempts to classify flowering plants (Angiosperms), morphological characters, particularly those of flowers and fruits, have been crucial to define natural groups. Since the introduction of DNA sequences as the basis of modern molecular phylogenetics—for instance, APG IV (2016) and Zuntini et al. (2024)—the role of comparative flower morphology has changed (Jeiter & Smets, 2023, 2024). Despite these changes, comparative morphology and developmental studies in particular, remain an important source of data for evolutionary studies in Angiosperms.

Scanning electron microscopy (SEM) and light microscopy are the standard methods for observing development (also called ontogeny), recently complemented by micro-computed X-ray tomography ( $\mu$ CT; Ledford, 2018). For those who do not have access to scanning

electron microscopy, epi-illumination light microscopy may be a useful alternative (see, e.g. Charlton et al., 2011; Sattler, 1968).

The different stages of development are necessary to enable comparative research. It is therefore essential to take the right samples. Years of experience have taught us that sampling for developmental research requires a certain amount of understanding of the subject and a certain amount of experience that is not easy to communicate. When collaborating with colleagues unfamiliar with comparative morphology, it is logical that important quality criteria are often not met, resulting in incomplete sampling and needless damage to the plant without generating valuable data. Proper sampling is not only crucial for ontogenetic studies but also benefits related fields such as Evolutionary Developmental Biology (EvoDevo), a comparative discipline that aims, among other things, to map the genes responsible for the development of, for

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example, flower organs (Wanninger, 2015), thereby also contributing to a better understanding of the homology (similarity due to a common evolutionary origin; Ochoterena et al., 2019) and the evolution of structures. Given the challenges of collecting the required material, we want to stress the importance of proper sampling techniques for flower and fruit developmental research. As Jeiter and Smets (2024) pointed out, the knowledge and expertise of ontogenetic research should be made available to the next generations of morphologists and systematists. This article provides essential guidelines for reliable and reproducible sampling for ontogenetic studies, supporting researchers and collaborators interested in contributing to this field. Although our focus is on flowers and fruits, the methods described can be adapted to other parts of plants.

## 2 | WHAT TO COLLECT?

Collecting material for flower and fruit ontogenetic studies has its peculiarities because not only open flowers (also called anthetic flowers) or mature fruits are required but stages covering the whole range of their development are equally important. In addition, some developmental stages occur only briefly during the growth of a flower or fruit and may withhold vital information about the homology of the trait and the evolution of the species. Therefore, it is important to ensure an adequate coverage of developmental stages allowing for a complete reconstruction of flower and/or fruit development. This is particularly important if the material is collected from the wild and the species cannot be sampled again without a major investment of time and money (see below 'Where to collect?').

The stages and time of development of a flower from initiation to opening vary greatly from species to species. In a classic paper by Smyth et al. (1990), the authors describe in detail the early development of the *Arabidopsis thaliana* flower in 12 stages, while the development of the flowers from their first appearance to the shedding of the seeds is divided into 20 landmark events and takes about 13 days (see Müller, 1961). A similar approach with 20 stages has been adopted more recently by, for example, Brukhin et al. (2003) and Alvarez-Buylla et al. (2010).

The stages of flower development vary considerably between species. As we are not aware of a generally accepted definition of flower and fruit developmental stages, we propose six stages to help communicate sampling requirements to colleagues and students:

- **Early flower development (Figure 1a)**, when the flower itself and the floral organs are initiated. The pattern of organ initiation holds much critical information for evolutionary studies. In general, primordia occur in spirals or whorls with a variable number of members; sepal primordia are the first to initiate, followed by petal primordia, stamen primordia and carpel primordia. The number

and position of these primordia on the floral apex are very variable between species of different taxa. Primordia may be freely initiated, or from the earliest initiation, primordia may be fused within a whorl, as is often the case with carpels.

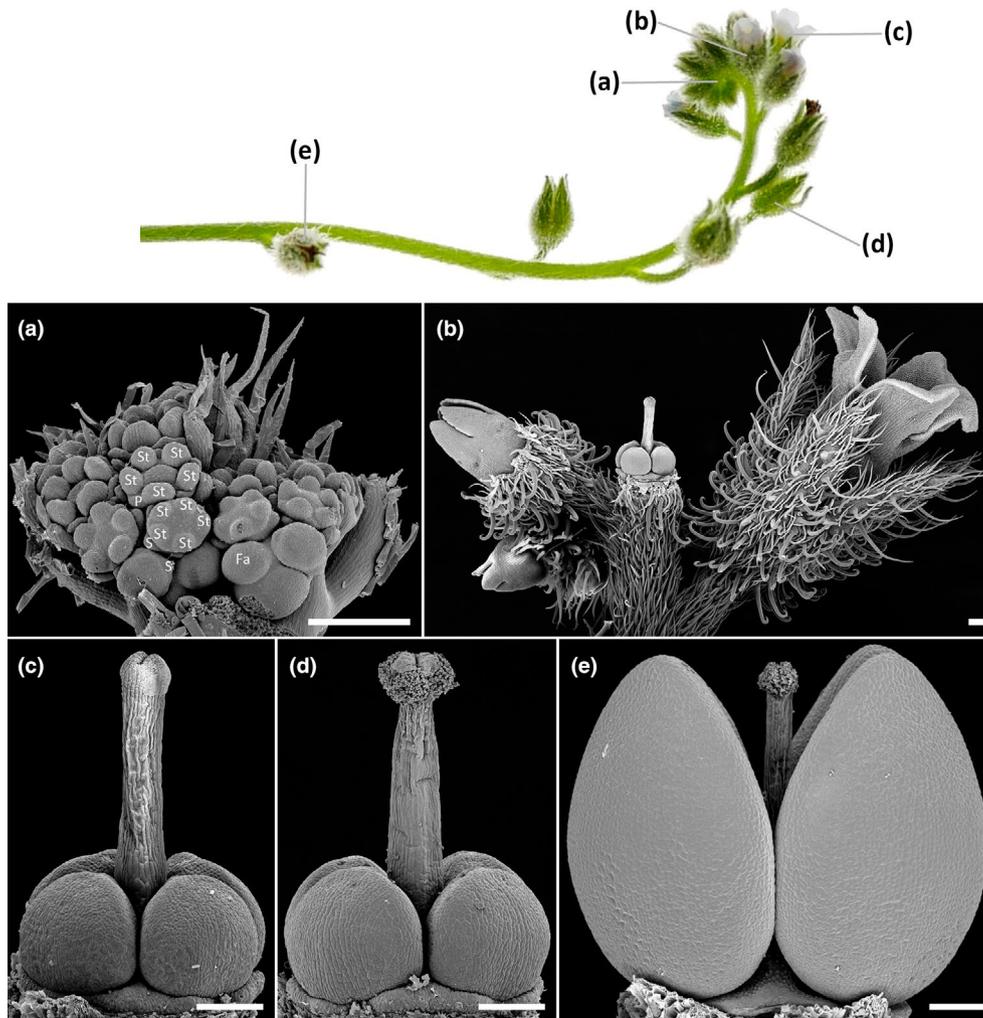
- **Mid-developmental stages**, when floral primordia differentiate. In species with a differentiated perianth, sepal primordia develop into sepals and petal primordia into petals. In species with undifferentiated perianth, tepal primordia develop into tepals. Sometimes petal primordia may differentiate before sepal primordia, but generally, petals differentiate after sepals. Sepals, petals or tepals may fuse within a whorl. Stamen primordia differentiate into filaments and anthers and initially free or fused carpel primordia develop into ovaries, one or more styles and one or several stigmata and petal primordia flatten and assume their final shape.
- **Late-developmental stages (Figure 1b)** are characterised primarily by the enlargement and elongation of the differentiated floral organs. In many cases, elaborations of floral organs such as scales on petals, secretory tissues such as nectaries and oil glands, or trichomes appear in the mid to late stages of development. Late flower development ends with anthesis, the opening of the flower.
- **Anthesis (Figure 1b,c)** may be accompanied by developmental processes such as protandry or protogyny. The switch between both phases might be accompanied by movement and/or growth of floral parts or entire organs.
- **Fruit development (Figure 1d)** includes the stages between anthesis and fruit maturity. The development of fruits is a complex process with huge differences between species in the timing and differentiation of the fruit wall and other floral organs, sometimes also involving the pedicel, bracts or entire inflorescences.
- **Fruit maturity (Figure 1e)** is reached when the seeds are mature and ready to be dispersed. Seeds may remain enclosed in the pericarp and additional structures, or they may be released.

Depending on the research question and the variability of the group under study, certain stages may not be necessary. However, in most studies of flower and/or fruit development, all stages and as many intermediate stages as possible are required, so collecting sufficient material is of prime importance. Some exemplary studies showing all the important flower developmental stages are Endress (1997), Sajo et al. (2017), Vasile et al. (2022), Jeiter et al. (2023), Zhang et al. (2023).

A voucher specimen must be collected from each population sampled for flower and fruit developmental studies and deposited in a recognised herbarium. These vouchers make it possible to check the identity of the species at a later date, if necessary, or to use the specimen for the collection of other data (e.g. DNA).

## 3 | WHERE TO COLLECT?

The main places for the collection of material for developmental studies are in the field and in living collections, such as botanical



**FIGURE 1** SEM-images of developmental stages of an inflorescence, flower and fruit of *Myosotis arvensis*, Boraginaceae. (a) Early developmental stages at the inflorescence tip. Fa = flower apex; P = petal primordium; S = sepal primordium; St = stamen primordium. (b) Pre-anthetic and anthetic flowers. Sepals and stamen-corolla tube of an anthetic flower were removed to view the gynoecium. (c, d) Sepals and stamen-corolla tube removed. (c) Gynoecium at anthesis. (d) Gynoecium after anthesis and onset of fruit development. (e) Mature fruit. Scale bars = 100  $\mu\text{m}$ .

gardens. Collecting in the field is by far the best, as the species can be observed in their natural environment. It does, of course, require the necessary permits, knowledge of local nature legislation and protected species, and an awareness of possible obstacles, hazards and dangers. Note that local institutions can provide a lot of information and possibly also guidance.

Plants in botanical gardens are easier to sample repeatedly, but if a particular stage is missing, as in the wild, resampling may not be possible until the next flowering period, which can take a year or even longer. Furthermore, plants in gardens sometimes develop slightly differently from those collected in the wild. This may be due to inbreeding, hybridisation or unusual growth conditions.

Collecting in botanical gardens is, of course, more convenient and permits are often easier to obtain as research is one of their main aims. Plants in botanical gardens have accession numbers and associated voucher specimens. These may be in their possession or deposited in a natural history institution.

Natural history museums and botanical gardens also often have alcohol collections from previous field campaigns or research projects, and it is advisable to consult these before going into the field.

Herbarium collections are often not considered the best for collecting flowers for developmental studies, as the specimens are pressed and dried, two conditions that are not desirable. For very rare material, or when collecting in the wild or the garden is not possible, herbarium specimens may offer a solution. Samples taken from herbarium specimens can be rehydrated which may even restore their 3D-structure. One method is to boil the flowers in water with a bit of detergent but this quick and dirty method often does not give satisfactory results. Ayensu (1967) introduced a method in which air-dried plant material is rehydrated in sulfosuccinic acid 1,4-bis (2-ethylhexyl) ester sodium salt and then sectioned for light microscopy. Erbar (1995) successfully tested this method on air-dried buds taken from herbarium samples which she then prepared for SEM observation. This technique has been applied successfully

for example in observing the floral ontogeny of *Sphenoclea zeylanica* (Sphenocleaceae; Erbar, 1995) and several species of *Croton* (Euphorbiaceae; Thaowetsuwan et al., 2024).

## 4 | WHEN TO COLLECT?

The duration of flower and fruit development varies greatly between taxa. It can last from a few days up to a year or even longer. It is surprising how quickly after the flowering season of some species, the buds for the next flowering cycle are already in place (especially in shrubs and trees, see Figure 2a,b). Also, in some species, flower development from onset to fruit maturity happens more or less simultaneously within an inflorescence; in others, successively, which is a great advantage because, with a bit of luck, one inflorescence will offer many developmental stages (Figure 1).

Environmental triggers of flowering such as El Niño rain events in deserts or wildfires should be considered as some species are particularly adapted to these events. Flowering time will have a major impact on sampling and needs to be carefully considered before starting a sampling campaign. For some taxa, several collection trips

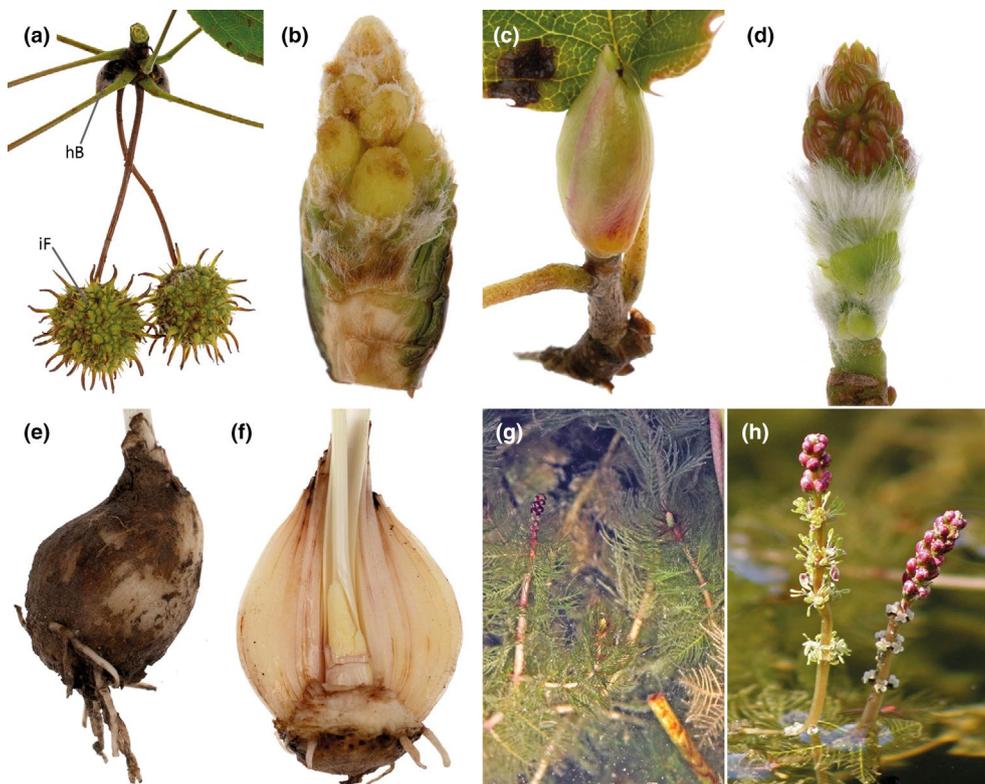
may be required to ensure adequate coverage of all the necessary developmental stages, which is relatively straightforward if sampling can take place in living collections, but less obvious if field trips have to be planned. This makes the planning of a field trip very important, as species do not flower at the same time, especially in regions without a clear seasonal pattern.

## 5 | HOW TO COLLECT?

### 5.1 | Materials required

A list of equipment and materials useful for collecting is provided in the following paragraphs (Figure 3). This list is not exhaustive and, as usual, the actual equipment for collecting will depend on the taxa in focus.

- *Pruning shears* (Figure 3a) may be essential for larger specimens and thick stems or fruit stalks. For trees, lianas, epiphytes and other plants in high, hard-to-reach locations, long-reach pruning shears or a slingshot may be required.



**FIGURE 2** Exceptional cases of flower development. (a–d) Flowers develop in hibernation (winter) buds. (a, b) *Liquidambar acalycina*, Altingiaceae. (a) Apex of a branch in early October. Two hibernating buds (hB) and two immature infructescences (iF) of the same year. (b) Scales and young leaves of a hibernation bud removed and young inflorescences exposed. (c, d) *Corylopsis gotoana*, Hamamelidaceae. (c) Apex of a branch in early October with a hibernating bud. (d) Scales and young leaves of the hibernating bud removed and flowers in late-developmental stages exposed. (e, f) *Muscari armeniacum*, Asparagaceae. (e) Intact bulb, freshly removed from the ground. (f) Half of the onionskins removed and two inflorescences in early developmental stages exposed. (g, h) *Myriophyllum spicatum*, Haloragaceae. Images: L. Eckert. (g) Mid and late-developmental stages submerged under water. (h) Inflorescences raised above the water surface with anthetic male flowers (left) and anthetic female flowers (right).



**FIGURE 3** Items required to collect material for flower and fruit developmental studies. (a) Pruning shear. (b) Scissors, tweezers, pocket knife, hand lens, razor blades, probe, field book, pencil, permanent marker, stickers. (c) Ziplock bag and paper towels. (d) plastic bottles and containers ranging from 20 mL to 1 L. (e) Plant press to collect voucher specimens. All items are to scale.

- Tweezers, scissors, pocket knives and razor blades (Figure 3b) are required to remove small samples and fragile flowers and to clear the material from leaves or bracts.
- Ziplock (Figure 3c) or ordinary plastic bags are fine for keeping samples fresh for a short time, for example, when climbing a tree or rock face, where carrying, opening and closing a liquid-filled bottle may be too difficult or even dangerous. Ideally, a few drops of water or a damp paper towel should be added to the bag to create a humid atmosphere and prevent the samples from wilting. Ziplock bags have the advantage of being airtight. Inflating the bags like a pillow will prevent them from being crushed. Paper towels are always useful in the field. In some cases, it may be helpful to place a towel or two inside the bottle of samples to limit movement during transport.
- Plastic bottles or containers (Figure 3d) with a wide opening are best for collecting samples in the fixative (see below). They are less likely to break if dropped. It should be avoided to force samples through a narrow opening. Although the flexible, fresh sample may survive this without external or internal damage, once fixed, samples are far less tolerant and may break, crack or crush if forcefully removed from the bottle. Bottles come in a variety of sizes and volumes. For flowers and developmental stages, 100–200 mL bottles should be sufficient. Larger fruits will require larger containers.
- Plant press (Figure 3e) and newspapers are important for collecting the voucher specimens. A voucher specimen should be collected for each population from which samples have been taken. More information on collecting herbarium specimens can be found in

the Herbarium Handbook (Davies et al., 2023) and on <https://www.botanicgardens.org.au/sites/default/files/2023-06/How-to-collect-plants.pdf>.

- *Silica gel*, *airtight containers* and *envelopes* are needed to collect some leaves for DNA extraction. It is advantageous to have the DNA corresponding to the exact morphological samples collected for subsequent morphological, allometric or morphometric analyses, for which the phylogenetic background is important.

Fixation of the collected material is a critical step. It prevents the material from drying out, rotting and moulding, and it prepares the samples for further analysis in the laboratory. It is recommended to keep the collected samples in a substantial excess of fixative for at least 1 week, but longer storage should not cause any problems and should ensure complete fixing of all external and internal structures and tissues.

There are several different fixatives in use for different research questions (Megías et al., 2024). Two fixatives have proven to be reliable for general flower and fruit development: ethanol and a solution of formaldehyde, acetic acid and ethanol (FAA; see [Data S1](#)).

As for ethanol, 70% denatured ethanol is most commonly used, but a solution with an ethanol concentration of at least 50% and a maximum of 80% should work fine. The concentration of ethanol influences two qualities of the samples: the higher the ethanol concentration, the more brittle the samples become and the more the samples shrink. Lower ethanol solutions may result in overly soft and mushy samples, although shrinkage is reduced. Ethanol has the advantage of being more frequently available globally and, in some cases, the material might be fixed in high-ethanol spirits such as rum (up to ~80%).

The formaldehyde in FAA denatures proteins and cross-links the denatured proteins, thus creating a more stable, but also more brittle sample, which can be advantageous for downstream analyses, especially when section-based anatomical studies or critical point drying are planned. To reduce volume and weight when travelling, and if FAA is not available in the region where the collection campaign will take place, preparing a solution containing only formaldehyde and acetic acid in the correct proportions has proven to be the easiest way to use FAA in the field, if it is permitted to carry these agents. In the field, this solution can be mixed with 70% ethanol to produce FAA ([Data S1](#)). Note that formaldehyde is carcinogenic (IARC Working Group on the Evaluation of Carcinogenic Risks to Humans, 2006). Exposure, especially to its vapours, should be avoided or at the least reduced to an absolute minimum. Formaldehyde and other ingredients of fixing solutions might not be available where collection takes place or obtaining the ingredients might be a disproportionate effort.

Finally, as always, it is extremely important to keep good and complete field records of what is collected, when and where; it should be noted in detail which developmental stages have been collected and which may be lacking. The numbering of all bags, bottles with pencil-written labels and papers written in pencil inside the containers cannot be emphasised enough.

## 5.2 | Helpful tips

Collecting the right samples is, of course, a prerequisite for any sampling campaign. However, there are other practical aspects to be considered when collecting for developmental studies that have to do with the delicate nature of the samples.

- When a plant is flowering, inflorescences should be collected at the youngest possible stage, even if there are no flower buds visible to the naked eye. Most inexperienced researchers who start collecting flower buds for developmental studies tend to collect identifiable flower buds, but in many cases, these are already in the mid or late stages of development and just need to enlarge and open.
- Once observations begin in the laboratory, it may be necessary to go through a lot of material to find the required stages of flower development; consequently, many flower buds at different developmental stages may be needed. It is therefore important to collect a lot of material to ensure that all the necessary stages are covered and to have a buffer for flowers with damage, varying numbers of floral organs in the whorls of a flower, or, more generally, to allow for errors and accidents that may occur during subsequent preparation and analyses (failed critical point drying, samples that have dried out, etc.). Plant species may be rare, endangered, protected, difficult to cultivate or susceptible to infections when damaged. These limit the amount that can be taken either from the wild or living collections. A collector should always behave reasonably when sampling threatened species in the wild. A good practice on how to handle collecting Orchidaceae can be found in Singer et al. (2024).
- Early and sometimes mid-developmental stages are often concealed to protect the soft tissues of the developing flowers from external influences and herbivory. They may be enclosed in hibernating buds ([Figure 2a–d](#)), leaf axils and sheaths and underground ([Figure 2e,f](#)) or underwater ([Figure 2g,h](#)). A good understanding of the onset of flower development of the focal taxa is required so that a plant with hidden early developmental stages is not mistaken for vegetative.
- Early developmental stages of solitary flowers are usually the most difficult to find. It is often a matter of luck whether the visible young flower shoots are in the early stages of development or whether the shoot tip is vegetative.
- Late-developmental stages are often easier to collect and, depending on the research question, a dense coverage is not as critical as in studies where early developmental stages are essential. However, there are many cases where flowers even close to anthesis are concealed ([Figure 2a–d](#)). In the rarest cases, even anthetic flowers might flower underground (Kuhnhäuser et al., 2023).
- Samples for fruit developmental studies are generally easier to collect. Underground fruiting happens, but usually, flowers are produced above ground and their fruits are thus easier to find and collect.

- Large inflorescences or stems should be cut, not bent. Bending structures that are larger than the bottle will cause pressure and deformation. Cutting larger structures into pieces that fit easily through the bottle opening will simplify subsequent handling. Superfluous structures such as long inflorescence axes, large bracts or long pedicels should be removed before placing the samples into a container.
- Small inflorescences with small floral buds should be kept connected. If only individual buds can be collected, a longer pedicel or a piece of inflorescence axis will help with subsequent preparations. Pedicels or inflorescence stalks should never be completely removed as they help handle and hold the sample.
- If a bottle must be transported over a long period, it should be fairly full with samples and filled with fixative close to the lid. Stuffing the bottles with material should be avoided, as this will result in deformed, punctured or broken samples. Samples should be placed loosely in the bottle so that they do not slosh around, but are neither tightly packed nor stuffed.
- Practical problems may also occur when developing fruits are sampled. The most obvious one is fruit size. Even tiny flowers like the flowers of *Theobroma cacao* (Malvaceae) develop into enormous, massive and heavy fruits. Another possible obstacle is fruits that split or disintegrate at maturity. A mature fruit may not survive sampling, fixing or transport. Sampling pre-mature fruits helps to overcome this obstacle but may result in missing the critical developmental steps involved in fruit maturity and seed dispersal.
- Weight is often a limiting factor when shipping or transporting samples from the field to the home institution. An easy solution is removing most of the liquid from the container, leaving the samples dripping wet. After an appropriate time in the fixative, the samples should remain stable in the saturated atmosphere inside the airtight container and should survive even longer transport. At the destination, the containers can be simply refilled with ethanol (70%).

## AUTHOR CONTRIBUTIONS

Julius Jeiter and Erik Smets conceived the idea and wrote the article together.

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## CONFLICT OF INTEREST STATEMENT

No conflict of interest is declared.

## DATA AVAILABILITY STATEMENT

This article does not contain any data.

## RELEVANT GREY LITERATURE

You can find related grey literature on the topics below on Applied Ecology Resources: [Collecting](#), [Evolution](#), [Flower development](#), [Fruit development](#).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Data S1.** Instructions for preparation of FAA and FAA stock solution.

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