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Review

Hermetia illucens (Diptera: Stratiomyidae): Need, Potentiality, and Performance Measures

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Abstract: The research on black soldier fly (BSF; *Hermetia illucens* L.; Diptera: Stratiomyidae) rearing is on the rise. The larval ability to grow on organic substances makes it an ideal candidate for the bioconversion of agricultural and other organic side streams. While there are several publications on the variables influencing the growth and development of different stages of BSF, juxtaposing the results could be amiss. This is because of the different experimental approaches and units used by the researchers. A few publications also lack information that might be necessary for comparing the results when using similar substrate and rearing conditions. In this review, we have analyzed the studies on rearing variables such as the type of feeding substrate, substrate depth and aeration, substrate temperature, substrate moisture, pH, feeding rate, and larval density mainly, but not exclusively, for the larvae. For the adults, factors such as the cage size, fly density, light, ambient temperature, and relative humidity are considered. In addition, larval performance when fed with side streams is encapsulated. This provides a backbone for future researchers to identify the already assessed variables along with their range and encourages them to define and use standardized rearing practices for a better comparison of the results.

Keywords: black soldier fly; *Hermetia illucens*; insect rearing; rearing variables; side streams; circular economy; sustainability; insects as feed; alternative protein; waste reduction

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1. Introduction

In mimicking nature, insects can be deployed to convert low-value side streams into protein-rich insect-derived feed for animals [1]. Many industrial side streams are inedible by humans and cannot be applied as feed for conventional farmed animals but could be a source of feed for rearing insects [2]. The agricultural side streams have the potential to be used as feed for insects creating a sustainable circular economy [2,3]. The insects can then be directly fed or processed and fed to animals [4,5]. Insects are a valuable source of protein and fat for both humans and animals [1,6,7]. The additional advantages of using insects are [1,4] their rich nutritional profile, which meets the amino acid requirements for humans [8], fishes [4], and terrestrial animals [9], their lower GHG production [10], a lesser land requirement because of vertical farming, a shorter generation time, a lesser water consumption [6], a higher feed conversion efficiency, and their ability to thrive on side streams [11].

In the EU, insects have been allowed as protein sources for aquaculture since 2017 [12], and for poultry and pigs since 2021 [13]. The insects include the black soldier fly (BSF; *Hermetia illucens*; Diptera: Stratiomyidae), yellow mealworm (*Tenebrio molitor*; Coleoptera: Tenebrionidae), common housefly (*Musca domestica*; Diptera: Muscidae), lesser mealworm (*Alphitobius diaperinus*; Coleoptera: Tenebrionidae), house cricket (*Acheta domesticus*; Orthoptera: Gryllidae), banded cricket (*Gryllodes sigillatus*; Orthoptera: Gryllidae), field cricket (*Gryllus assimilis*; Orthoptera: Gryllidae), and silkworm (*Bombyx mori*; Lepidoptera:

Bombycidae). Insects are categorized as farmed animals and their feeding is subject to the same laws as conventional livestock. In the EU, some of these insects have also been proposed for human food. Albeit stringent regulation, the EU approved four of these insects; in the order of approval, the yellow mealworm, house cricket, migratory locust (*Locusta migrotaria;* Orthoptera: Acrididae), and more recently, the lesser mealworm.

In this review, the BSF is considered a potential insect for mass production. Through better knowledge of feed composition and the resulting larval composition, the nutrient profile of the larvae could be modified according to the requirements of feed production [14]. BSF is one of the seven insects for which larvae have been proposed to the European Commission for use in human food, although it has not yet been approved for such use. BSF is a polyphagous insect. Additionally, BSF larvae are not as susceptible to pathogens compared to other insects used for industrial rearing [15]. All the above-mentioned traits make BSF larvae the best candidate insect for industrial production.

The BSF industry plays an important role in feed safety, animal husbandry, garbage disposal, and environmental protection [1]. However, the mass production of insects, as a relatively new industry, has some challenges both in breeding and producing high-quality insects at low cost. The major problems that still exist are upscaling, unknown diet-specific feeding rate to reduce internal competition, lack of precise information on juvenile and later instar densities to maintain optimum temperature range for larval development, and preventing any disease outbreaks. For mass production, the major setbacks are automation and digitalization, the regulations that limit the use of certain feeds for insects, and their restricted sales [16]. Although protocols are available for industrial BSF breeding and rearing [11,17], there is a lack of information on handling the possible changes in the insect behavior on different feeding substrates. Despite scale (dimension) being an important factor that interacts with and influences the variables, the reliability of the BSF industry on the published laboratory scale studies can give unexpected results. The use of a variety of substrates that tremendously vary in terms of their properties, such as surface area to volume ratio, moisture, salinity, pH, or nutrients, makes it difficult to conclude on the best diet for the BSF larvae. In addition, the differences in the development time, fecundity, behavior towards specific environmental conditions, the yield, and the protein and fat production due to the insect strain are not well known for BSF [18]. The use of agricultural side streams, although sustainable, does not promise consistency in terms of product quality and nutritional value. This risk is higher if the agricultural side stream is seasonal and collected from several suppliers. Even with all the challenges, some progress has been made in understanding the biology of the BSF. Some of the information that is known on breeding and rearing BSF can be found in the life cycle section.

There are a variety of side streams available and tested as a feed material to rear insects and, in particular, BSF. However, an assessment of factors influencing larval production and a comparison of larval growth and development on side streams has not been summarized up to date. Therefore, this manuscript focuses on the abiotic variables essential for the optimum maintenance of all life stages. Additionally, a brief overview of the animal- and plant-derived substrates used as feed is given. The variables such as the type of feeding substrate, substrate depth and aeration, substrate temperature, substrate moisture, and pH are not applicable to adult flies in the majority of cases since they do not rely classically on feed but on their energy reserves to survive and reproduce successfully [17]. However, comprehensive information was gathered from the available literature. In addition, the volumetric factors, such as the cage size and fly density, are known to affect the fecundity, hence they are also listed in detail. Due to the overwhelming amount of BSF publications, the references cited are the most important representative studies and do not include all the data from every literature available so far. This work paves the way for the process of making BSF one of the mainstream feed sources by identifying insect feeds that are economical and environmentally friendly while highlighting different experimental approaches by researchers.

2. The Life Cycle of BSF

Adult flies, once emerged, live for approximately 9–11 days (d) when provided with no food, approximately 21 d when provided with water, and up to 50–73 d when provided with sugar water [19]. Besides the size, the sex of adult BSF can be determined by external dimorphisms, including antennal and abdominal structures (Figure 1i–m). The flies also need abundant sunlight or artificial lighting with a temperature range of 25–30 °C for mating and subsequent oviposition. The mating of the flies was observed at temperatures of 27 °C and above accompanied by bright sunlight conditions [20].

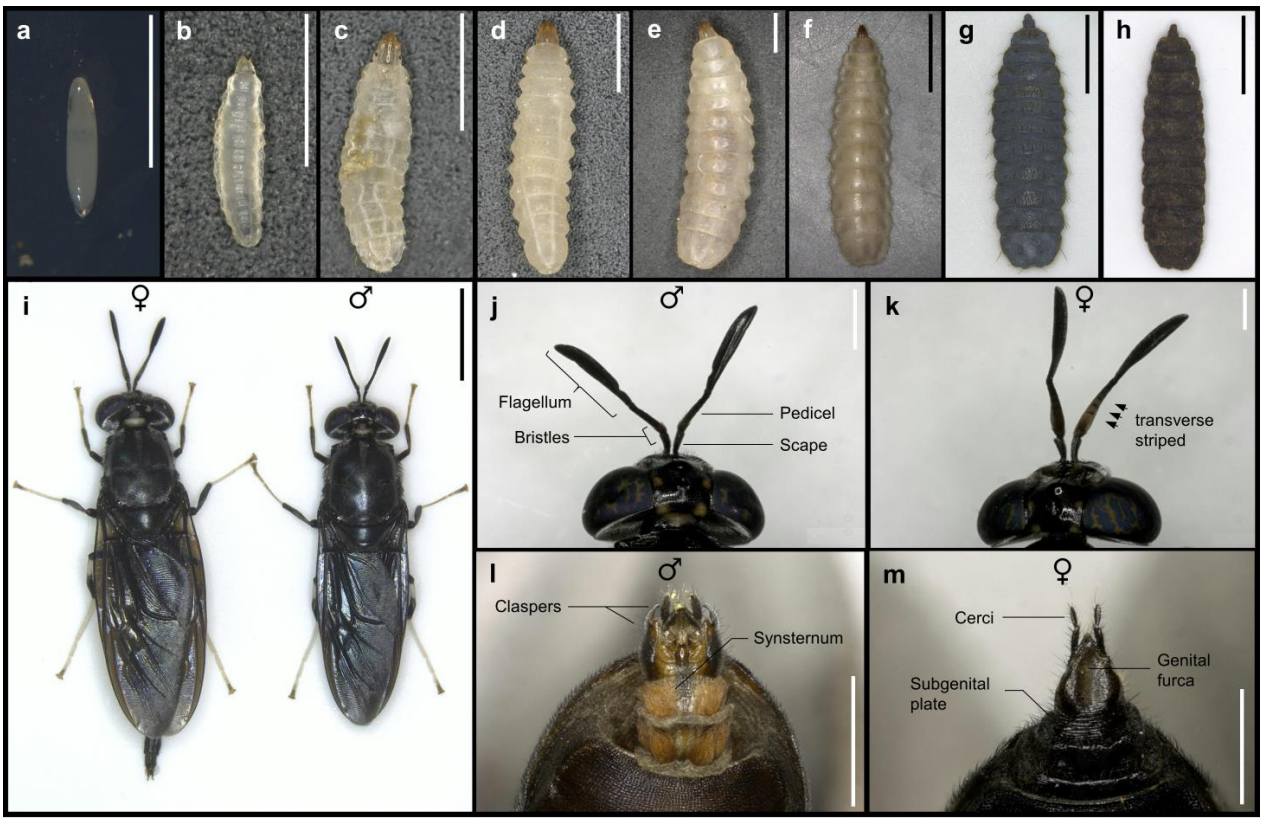

Figure 1. Life cycle and sexual dimorphisms of the antennae and abdominal genitalia of adult BSF. (**a**) Single deposited egg; (**b**–**g**) temporal sequence of larval instars L1–L6 (prepupa); (**h**) pupa; (**i**) full body view of adult female (left) and male (right) BSF; (**j**,**k**) dorsocranial view of male and female antennae; (**l**,**m**) ventrocaudal view of male and female genital structures (scale bars: white = 1 mm, black = 5 mm).

Mating occurs 2 d after fly emergence and up to 70% oviposition happens after 2 d of mating. Females lay approximately 120–820 eggs in clutches in dry spaces near decomposing matter using their ovipositor (Figure 1m) [21,22]. Up to 86.5% of oviposition was restricted to the noon hours (h) between 12:00 and 15:00, with a temperature range of 30–33 °C. The volatile compounds from decomposing materials [20,23], fresh fruit and vegetable waste [21,24], millet porridge mash [25], and the Gainesville diet [17] stimulate oviposition. Egg traps are used for the easy collection of eggs. The eggs turn white 12 h after laying (Figure 1a) and take 4–5 d to hatch at 24–27 °C and 70–90% relative humidity (RH) [20,26,27]. There are six larval instars (L1–L6) with the prepupa being the final one (Figure 1b–g). The first two instars are very fragile and the chances of mortality are higher during handling. Larval growth takes approximately 14–20 d under ideal climatic conditions with a nutritious diet [26,28]. Due to the larval mouthparts, ingestion is facilitated in a moist substrate with a smaller particle size. The fifth instar represents the reservoir of the highest nutrients and hence the desirable stage of harvest for animal

feed. Furthermore, larvae reach their highest biomass in the fifth instar. At the prepupae stage, the feeding stops and they move out of the moist substrate to pupate in a dry and safe space. Prepupae are dark brown to dark grey (Figure 1g). The longevity of the flies is also influenced by the caloric content of prepupae, which is diet-dependent. Higher caloric content in the prepupae extends the life span of the resulting adults by 4 d, as observed in wild BSF populations [26]. The pupation period is usually approximately two [29] to three [23] weeks under ideal conditions (Figure 1h).

3. Variables Affecting BSF Rearing

3.1. Type of Feeding Substrates and Corresponding Challenges

Saprophagous insects, particularly the BSF, can consume a diverse group of organic wastes [30]. Hence, BSF can be reared on a range of substrates, such as agricultural wastes [3,31–33], animal and human remains [34,35], fish wastes [36,37], food or kitchen waste [38–43], municipal organic wastes [44–47], compost leachates [30] as well as human [48,49] and livestock feces [29,50–54], and restaurant wastes [33,55] transforming them into a protein-rich biomass and residual frass that can act as a potent biofertilizer. Despite all the available side streams, there are some limitations. All types of organic materials are not allowed by the EU legislation to prevent potential dangers like the spread of zoonotic diseases. For example, side streams such as manure, catering wastes, slaughterhouse wastes, and unsold products from supermarkets and food industries (containing meat and fish) are prohibited as feeding substrates for insects in the European Union [12]. The main reason is the transmission of zoonotic diseases, especially by prions. The restrictions in the EU began due to bovine spongiform encephalopathy, which is a neurodegenerative disease in cattle [56]. Substrates currently being considered for insect feeding are dependent on availability, regulatory frameworks, and their feasibility of use [57]. To date, BSF producers in Europe are using poultry feed or pig feed as the main feed for BSF rearing. The increased demand for feed in recent decades is compensated by the import of feed ingredients such as soybeans. To meet export demand, forests and agricultural lands in developing countries are being converted to grow more feed crops [58]. Therefore, using these high-cost feeds raises the insect production price while competing with conventional feedstock. Moreover, using high-quality feed for insects, although they can grow perfectly well on low nutrient-based feed, is a waste of resources. Identifying a sustainable feed that is nutritionally ideal for the larvae and permitted by the legislation of the respective country can therefore be challenging. Feed for insects is often conceptualized based on the observed habits and habitat behaviors for that particular species in nature or in fields, rather than considering the nutrient requirements of the diet. Although observations of their natural behaviors in nature, for example, in feed consumption, give an idea of their preferred feed, nutritional composition would assist in optimizing growth and development [59]. The substrate selection for industrial-scale insect production must be performed based on its local availability, its suitability for larval growth and development, and its positive impact on waste reduction by utilizing substrates that are usually discarded. Preferentially, using side streams as feed for BSF larvae can be profitable for the industries [60]. Substrate selection also relies on its properties and how it can be best prepared to feed insects. For instance, the substrates can be blended [61], heat treated [62], steamed [41], fermented [63–65], sterilized [66], or pretreated with probiotic microbes [67–69] before usage as feed for the larvae. Furthermore, substrate properties such as particle size, pH, and moisture retention are also to be considered to make the substrate ideal for larval growth and development. Another challenge is separating the larval biomass from the feeding substrate; this is discussed in more detail in the chapter on substrate moisture. This leads to the exploration of factors that are crucial in rearing insects and how larval and adult performance responds to relevant substrate modifications.

3.2. Substrate Depth

Substrate depth is the height of the feed in which larvae live until harvest. Substrate depth is considered to influence larval development as it can affect larval movements, oxygen availability, and intraspecific competition. Larvae fed on mixed organic waste were studied for three weeks on the effect of feed depth and larval aggregation temperature [61]. A homogenized feed with a 5 cm depth had 60% of the prepupae, including the highest weighing larvae (approximately 270 mg FM) and a waste reduction of approximately 63% dry mass (DM) in comparison to all other feed depths (10, 15, and 20 cm). A feed depth of >10 cm prevented access to all the provided feed. In addition, the larval survival rate also decreased to lower than 80% as the feed depth increased [61]. Lopes et al. (2023) tested four substrate depths (1.0–6.5 cm) and also concluded that a substrate depth of higher than 5 cm impairs material reduction and bioconversion efficiency [70]. Generally, larvae accumulate in masses resulting in an increased temperature (due to metabolism and movement) known as the aggregation temperature. This temperature was highest for the homogenized feed with a depth of 15 cm. According to Brits (2017) and Lopes et al. (2023), to obtain a maximum waste reduction and higher larval biomass, the feed has to be homogenized and fed to the larvae at a 5 cm depth [61,70]. However, a depth of 5 cm is not a good option for upscaling production because of the space needed and the huge surface, which would lead to higher evaporation. Therefore, it is recommended to adjust the feed depths to <10 cm [61]. Peng et al. (2022) concluded that for the examined substrate depths of 10–20 cm, the bioconversion efficiency of pig manure is higher at the lower depths of 10–15 cm [71]. A depth of 3 cm is suggested to be the best in terms of biomass conversion efficiency and larval yield [70]. In a study by Lalander et al. (2020), the substrate depth was between 3.2 and 8.0 cm for substrates with a moisture content of 76% and ~98%, respectively. The corresponding larval survival rates were 19% and 97%; which might be the result of synergistic interactions between depth, aeration, and substrate moisture [72].

Substrate depth could also apply to neonates [21] and pupae [73,74]. A pupation substrate is not mandatory [75] but having wood shavings [3,22,73], sand or soil [22], vermiculite [74,76], or wood chips [74] prevents desiccation and was reported to support adult emergence. For instance, the percentage of fly emergence was only approximately 88% without the use of pupation substrate and increased to approximately 97% with the use of sand, topsoil, wood shavings, and potting soil. The duration from the prepupae stage to adult emergence took 17 d without any pupation substrate and sand in comparison to approximately 15 d for topsoil, wood shavings, and potting soil [22].

The limited literature makes it difficult to identify an ideal substrate depth, especially since studies usually examine specific depth ranges under different rearing circumstances. In addition, interaction with other variables such as the moisture content, homogenization level, and aeration might play a role.

3.3. Substrate Aeration

The performance of larvae could be influenced by the aeration within the substrate which in turn depends on the stickiness [21], viscosity [77], particle size [28,78], and physical properties of the feed, such as its fibrous nature [79]. The particle size range described in the literature includes 0.1–1.5 mm [75], ~0.4 mm [33], ≤1–15 mm [80], ~1 mm [63], ~5 mm [81], 4.00–6.35 mm [78], 1–2 cm [23], and ≤3.8 cm [82]. According to Dortmans et al. (2017), the substrate has to be shredded to a particle size of at least less than 1–2 cm in diameter [23]. Larval weights were slightly higher at a 6.35 mm (25 mg DM) particle size than at 4.00 mm (~23 mg DM), when fed almond hulls for two weeks [78]. The authors explain that the increased access of the feed to microbes and reduced oxygen transport are assumed to be reasons for lower larval weight with a smaller particle size [78]. Yakti et al. (2023) found that the larval weight reduced from ~125 mg FM to ~75 mg FM as the straw particle size decreased from >3 mm to ≤1 mm [80]. Usage of a blended substrate could result in less accessibility of feed for the larvae due to high feed compactness and lower oxygen levels at the bottom of the rearing box forming anaerobic zones harboring corresponding

microbiota [61]. Thus, the optimal substrate depth correlates with its density. The inclusion of low compactness components such as sawdust and wood chips as matrix elements during larval rearing may increase porosity and absorption of excess water in the feed [82]. Using pupation substrates of lower compact density (e.g., potting soil and wood shavings) is recommended in comparison to substrates such as sand with high natural compaction [22].

Dried sugar beet pulp and a mixture of middlings and distillers' dried grains adjusted to a moisture content of approximately 73% were considered for studying the BSF larvae performance. According to the authors, the higher aeration in dried sugar beet pulp compared to the mixture of middlings and distillers dried grain was due to different substrate physical properties. Especially the higher fiber content in dried sugar beet pulp resulted in a higher survival rate of ~78% than in the middling mixture (~56%) and dried distillers' grains (~28%) [79]. In contrast to the former study [79], the larvae were found to prefer a coffee pulp bed that is dense and homogenous [77]. Larval dry weight and overall yield were increased by three and five times, respectively, with increasing aeration from the 0.04–0.36 mL/g feed DM/min of substrate. However, higher aeration rates of $\geq$0.95 mL/g feed DM/min of substrate demonstrated no significant difference in the larval weight or the overall yield. According to Palma and colleagues, higher aeration possibly benefitted the microorganisms competing for resources. The reduced yield in the low aeration approaches is presumably due to the competition for the already scarce oxygen between larvae and microbes. Larval growth and development are influenced by the depth of the feed due to the formation of zones and varied aeration. It is therefore important to consider the factors of aeration and microbial activity during BSF production [83]. The medium-range aeration of 0.19–0.26 mL/g feed DM/min was used by Palma et al. (2019) without highlighting its effect on larval consumption or growth rate. In addition, the room ventilation of 1.22–1.39 m^3/kg feed FM/h by channel fans has been used for the substrates with a moisture content of 90–97.5% [78]. Ventilation can help in reducing the substrate depth build-up and obtaining a drier residue that is important for the easy separation of larvae during harvest. Although water removal through active ventilation is possible, substrate moisture of more than 90% would demand higher resources in terms of energy, space, and workload for a smaller change in outcome. Substrates with less than 80% moisture content are predicted to need less than 1 mL/g feed DM/min ventilation to obtain a frass of approximately 50% moisture [72]. The aeration within the substrate can also differ based on the types of lids used. Most [21,72,84] but not all studies [15] use an open lid with or without mesh to preserve the substrate moisture.

Several substrates are used to stimulate directional oviposition but mostly as a source of volatile compounds and not considering the substrate depth preferred by the females if allowed to lay eggs directly on those substrates. In the case of direct inoculation, eggs are usually placed on the surface of the substrate. Hence, the substrate depth here is not an applicable variable.

Active aeration is usually not a regular practice in rearing BSF. Although, there are several advantages such as avoiding the formation of anaerobic zones or easy separation of larvae during harvest, the energy consumption and substrate desiccation might increase disproportionate to the benefits.

3.4. Substrate Temperature

The temperature ranges found in the literature were between 23–30 °C for L1–L5 instars, ~22–33 °C for larvae and prepupae, and 10–30 °C for all larvae, prepupae, and pupae. These developmental periods are categorized by the description from the papers. The temperature of the feeding substrate plays an important role in the growth and development of BSF (Table 1). As an example, larvae took 1.7 and 5.2 d longer, respectively, to reach a prepupal stage at 30 °C and 36 °C in comparison to 27 °C. The 36 °C group did not support the transformation of prepupae to pupae [28]. The larval growth period in cow manure was almost two months at a substrate temperature of 22 °C [36]. The total weight gain by BSF larvae was higher (4.7, 4.3, and 11.1 g FM) at 27 °C in comparison to 23 and

32 °C for chicken, cow, and hog manure, respectively. There was no significant difference in weight gain for hog manure between 28 °C and 32 °C [85].

Table 1. Effect of temperature on BSF weight gain on a grain-based diet.

Temperature (°C)	Individual Larval Weight (mg FM)	References
24.9	125	[86]
27.0	150 [1]	[28]
27.6	175	[86]
30.0	138 [1]	[28]
32.2	125	[86]

[1] Individual prepupa weight (mg FM).

Substrate temperature is directly related to the ambient temperature. On the other hand, it is also clear that there is some interaction between feed, the substrate temperature, and larval aggregation temperature resulting in a varied larval performance for the same diet (Table 1). This indicates that it is essential to rear larvae at different temperatures for the same diet to determine the effect of temperature on the preferred larval trait. However, the substrate temperature does not remain constant during the feeding trials. At the beginning of the trials with early instar larvae, the substrate temperature is more crucial and is dependent on the ambient temperature, while the larvae generate a higher amount of excess heat as they gradually develop. Temperatures can rise to 42 °C at a room temperature of 23 °C with a high larval density [21,87]. The temperature during the decomposition of organic wastes by the larvae also differs. The highest temperature of 39 °C was recorded during the first days of an experiment for the mixture of vegetable and fruit waste, while the lowest temperature was recorded for vegetable waste alone after 20 d (28 °C) [45]. None of the larvae survived at temperatures of 10 and 42 °C. Furthermore, prepupae and pupae are vulnerable even to 40 °C. At 30 °C, the pupal development was the shortest with 8–10 d depending on the diet. The period from hatching to fly emergence can be as low as 28–31 d at 30 °C to approximately 182 d at 15 °C. The temperature range of 30–35 °C revealed the highest survival in most life stages [88]. Although the slower developmental times are not beneficial for insect mass production, it is important to study the threshold temperatures that slow down the rapid metabolism but are not life-threatening to the insect.

Hence, to obtain optimum larval, prepupal, and pupal development, the temperature is a key regulator. Furthermore, the consideration of other rearing factors, in particular larval density and substrate moisture, is necessary as they might affect the substrate temperature.

3.5. Substrate Moisture Content

Ambient or relative humidity affects substrate moisture, which is the quantity of water in the given substrate. The amount of water could be provided at once at the beginning of a feed trial, also known as initial moistening [73,79,89], or at different intervals during the experiment [50]. Initial substrate moisture in rearing BSF larvae was studied within a range between 20 and 90% by various experimenters. The optimum substrate moisture for BSF development was found to be approximately 40–60%. Substrate moisture of at least 40% is essential for growth and development [50]. A 56% increase in larval yield was observed as the substrate moisture content increased from 48 to 68% [83]. Cammack and Tomberlin (2017) postulate that optimum moisture not only affected the yield but also shortened developmental times, and increased pupation and emergence rates. The larval development was a week faster and required 25–50% less feed at 70% moisture content in comparison to 55%. There was up to a 3% higher fly emergence at 70% moisture compared to the 55% diet [76].

Ewusie et al. (2018) used substrates with an initial moisture ranging between 61 and 91% [45]. In another experiment, pre-consumer (vegetable trimmings, spent coffee and tea residues, no meat) and post-consumer (leftovers with meat) food wastes, with substrate moisture contents of 70, 75, and 80% were considered [90]. Here, the differences in wet larval weight were negligible between the different moisture levels. Larval weights at the moisture levels tested varied between 119 and 125 mg FM for pre-consumer and 143 and 161 mg FM for post-consumer waste. In contrast, the post-consumer diet produced heavier larvae (~153 mg FM) compared to the pre-consumer (~122 mg FM) diet due to the higher crude protein (CP) content in the former and not because of the difference in moisture levels. The larval growth was found to be 3–5 d faster in 80% substrate moisture compared to 70 and 75%. However, the survival rate was not affected by the moisture content [90]. Although early instar larvae are more robust than eggs (Figure 1a–c), lower percentages of moisture in the pre- and post-consumer treatments resulted in the drying of substrates, disabling larvae from obtaining enough nutrients, and thus reducing growth and development [90]. Nguyen et al. (2013) examined substrates with moisture contents between 75.2 and 96.5% but the effect of moisture on larval performance is not specified [39]. A broader moisture content range between 20 and 90% studied at 10% intervals by Fatchurochim et al. (1989) revealed differences in survival rates on moistened poultry manure [50]. The BSF survival was best and similar for the substrate moisture ranging between 40 and 60% in comparison to lower (20 and 30%) and higher ranges of moisture (70, 80, and 90%). As opposed to other publications, the 70% moisture reduced the BSF survival rate to 38.8% but the weight of the adult flies was the highest (4.4 mg DM) [50]. The survival rates between different life stages can vary depending on other factors besides rearing in the moist substrate [15]. A few studies also use structuring compounds in the feed such as sawdust [91], or wheat bran and brewers' spent grain [92]. Generally, pupae are able to survive and eclose without any pupation substrate. In spite, a study testing pupation substrates of varying moisture (dry to 150%) concluded that its use does affect prepupae mortality and formation of pupae. According to the authors, moistened substrates reduced the prepupal mortality by $\geq$88%, whereas dry pupation substrates enhanced the pupation rate by up to 9%, compared to the groups without pupation substrates [74].

Similarly, the use of substrate for the egg stage is limited unless the eggs are immediately inoculated onto the substrates [3,28,36]. The direct inoculation of eggs on substrates with 60–70% [17,28,91] may lead to reduced hatchability [17]. Providing water for flies is recommended by most studies. This is performed by either spraying water on the cages [17,45] or by keeping a water source like a wet cotton wick [76].

Substrate moisture is a crucial factor not only for BSF growth and development but also for larval harvest, especially in an industrial setting. In conventional bioconversion studies, organic wastes have been used as such without adjusting the water content to the requirements of the BSF [46]. Although this could save time, separating residues at approximately 80% moisture is considered difficult to impossible. Feeding larvae daily reduces the sieving efficiency as the FM feed is mostly moist [72]. Thus, reducing the substrate decomposition rate resulting in the emission of a foul smell because of incomplete substrate degradation. Larvae also tend to escape from the moist substrate. Usually, the substrate moisture decreases with ongoing rearing because of larval movement, mixing of the substrate, evaporation, and assimilation of nutrients. Increasing moisture content is crucial for some substrates, such as almond hulls, for breaking down the particles by larvae and associated microorganisms [83]. BSF larvae can ingest the nutrients dissolved in water with ease when the substrate moisture is maintained at approximately 70% [45].

Although substrates with higher moisture content could be fed to the larvae, the use of substrates with less than 80% moisture is recommended for proper larval development and is favorable for separating larvae from frass [72]. Egg hatching does not require a moist substrate, albeit few studies inoculate the eggs directly onto it. Therefore, an optimal moisture content cannot be suggested based on the current studies.

3.6. Substrate pH

There are only a few studies on substrate pH and the corresponding effects on larval growth and development, and almost none on the effects on hatching when eggs are placed immediately onto substrates. Therefore, the influence of pH on BSF growth has not been fully elucidated, although available studies have included pH values ranging from 2.0 to 10.0. Ma et al. (2018) showed that the performance of BSF larvae is pH-dependent [93]. While the pH of the diets differed considerably at the beginning of feeding, it was observed that pH values settled between 8.9 and 9.4 at the end of feeding (Table 2).

Table 2. Change in pH and corresponding individual larval weight on different diets.

Feed	Initial pH	Duration (d)	Final pH	Individual Larval Weight (mg FM)	References
Gainesville diet	4.0–9.5	9.7	8.9–9.4	140–150	[94]
Coffee pulp	7.6	13.0	8.9	147	[95]
Chicken feed	~5.0	22.3	7.2	240	[75]
Cottonseed press cake	~6.0	23.7	8.9	140	[75]
Dairy manure	8.2	21.0	7.3	-	[96]

Both acidic and alkaline pH values were well-regulated and resisted by BSF larvae [94]. The increase in pH may be due to the release of ammonia in substrates rich in nitrogen [85,97]. The pH seems to be affected by the feeding rates or the feed amount because the measured pH of the substrates (vegetable wastes) at lower feeding rates of 60 mg FM/larva/d remains more or less constant between 7 and 8. However, higher feeding rates such as 200 mg FM/larva/d possibly create an anaerobic condition pulling the pH to acidic values ranging between 4 and 5. The acidity was assumed to have lowered the growth performance of the larvae [43]. Interestingly, two nutritionally differing diets with pH values in the neutral (6.8) and slightly acidic (4.5) range showed no difference in pH levels within the larval gut. The pH values in the anterior, middle, and posterior midgut of larvae on both diets were approximately 5.5, 2.0, and 8.5, respectively [81].

The pH of fresh dairy manure was 8.2 [96]. Conversely, the initial pH of pig manure was 6.0–6.2, whereas that of chicken manure ranged between 7.4 and 8.2 [85]. Here, the harvested larval weight was 2.4-fold higher in hog manure than in chicken manure at 27 °C. According to the authors, the difference in pH probably affected some antimicrobial peptides influencing larval growth [85]. The pH of a diet consisting of chicken manure and dairy manure in the 2:3 ratio used by Ur Rehman et al. (2019) was 7.6 [67]. The pH of the fresh pig manure used in a choice test against a plant-based side stream diet ranged between 6 and 7, while the plant-by-product was between 3 and 4. It is unknown if the larval choice for pig manure was based on their aversion to the sensed acidity from the other feed [98].

There are several studies giving initial pH values but without further relationships between pH and life-history traits of BSF larvae [67,96,98]. Understanding the changing pH during larval rearing might help to optimize the dietary composition and feeding rates.

3.7. Feeding Rate

The feeding rate is defined as the amount of feed provided to the larvae or adult flies at a given time to support their growth, development, and maintenance. There are numerous studies focused on feeding, but only a few that address feeding rates for the successful production of BSF larvae. Larval feeding could either be performed initially in one batch [48,93,94] or at regular intervals during the experimental duration. The continuous feeding interval varies across the studies from daily feeding [76,94] to feeding once a week [84] or in other intervals [41,48,72]. Studies using continuous feeding either replace the feed completely at defined periods [84,99] or add a new feed on top of the remaining feed [48,53]. The feeding

aspect also differs in terms of quantity. The feed could be provided at defined feeding rates [53,89] or ad libitum [15] and sometimes with no information on the total amount of feed [2,86]. The feeding rates included in the studies ranged from 12.5 mg FM/larva/d to approximately 1000 mg FM/larva/d (Table 3).

Table 3. Larval feeding rate in various studies.

Feeding Rate (mg FM/Larva)	Duration (d)	References
60	144–215	[53]
350	15	[79]
960	12	[94]
1000	19–21	[67]
1667	21–29	[93]
13–200 [1]	10–36	[100]
13–200 [1]	38–45	[32]
50–200 [1]	15	[61]
70–170 [1]	20	[89]
90–230 [1]	~25–30	[52]
100 [1]	29–43	[99]
100–1000 [1]	12	[48]
200 [1]	12–19	[101]
~286 [1]	-	[84]
~40–73 [1]	-	[39,40]

[1] Feeding rate in mg FM/larva/d.

For enhanced prepupal growth, the frequency of adding feed is more impactful than the amount of feed itself [48]. If the final product is a protein with the desired amino acid profile and fat, a feeding rate of 125 mg FM/larva/d or higher was recommended by Brits (2017). For a faster yield that results in early prepupae formation, i.e., 60% of prepupae within 21 d after hatching, the feeding rate can be raised to 200 mg FM/larva/d. Larval biomass did not significantly differ between both feeding rates. However, the efficiency of the conversion of digested feed is highest at the 125 mg FM/larva/d (42.2%) in comparison to ~32% for the 200 mg FM/larva/d feeding rate [61]. In a study by Myers et al. (2008), larval performance varied when cow manure was fed at different feeding rates of 90–230 mg FM/larva/d, with the highest feeding rate resulting in the greatest larval weight (~178 mg FM) and the highest prepupal fresh weight (~137 mg FM), faster larval development (~25 d), and the highest adult fresh weight (~55 mg FM) [52]. In contrast, the lowest feeding rate resulted in ~142 mg FM of larval and ~89 mg FM of prepupae, ~30 d for larval development, and ~37 mg FM of adult weight. A feeding rate of 100 mg FM/larva/d chicken feed resulted in prepupae of 48 mg FM with a substrate degradation of ~42%. The feeding rate of 200 mg FM/larva/d produced 63 mg FM prepupae with a substrate degradation of ~26% [100]. In another study, 200 larvae were fed with homogenized rice straw powder at rates of 12.5, 25, 50, 100, and 200 mg FM/larva/d. In the latter feeding rate, the prepupae weight was highest with 13.6 mg DM after 38 d of rearing compared to ~2 mg DM in the lowest feeding rate after 54 d. At 200 mg FM/larva/d, the substrate consumption was merely ~10% in comparison to the feeding rate of 12.5 mg FM with 30% substrate consumption harvested at 50% prepupal formation. This confirms that, independent of the feeding rates, the harvested weights are very small and not suitable [32]. According to Parra-Paz et al. (2015), feeding up to 163 mg DM/larva/d and maintaining a density of two larvae/cm^2 is considered ideal based on the predictions from modelling in terms of biomass gain (59 g DM/m^2/d) and waste reduction index (2.6%/d) without decreasing the pH to acidic levels [43]. Klammsteiner et al. (2021) fed larvae with oil waste at 70 mg FM/larva/d and food waste at 170 mg FM/larva/d to obtain the same organic matter as in 100 mg FM chicken feed per larva [89].

After the larvae have been fed for a certain period, insects must be harvested or separated from the remaining frass. This procedure is performed either by handpick-

ing them [53] or sieving [79], usually depending on the substrate moisture at the end of the experiment. In addition, the harvesting also varies in terms of the developmental stage. For example, harvesting was conducted at the L5 stage [102] when the first prepupae were found [103], or at 10–100% prepupae formation [82,84,104], or at the pupae stage [105]. However, other studies predefine a harvest date that could range between 8 d [80] to 20 d [89] or allow the prepupae to self-harvest by actively crawling out of the substrate [24,96]. The emerged flies are not fed in the conventional sense but are commonly offered water to drink. However, providing substances like sucrose solution [73,106,107], moistened sugar cubes [19], honey, D-Glucose, *Spirulina* or *Chlorella* powder [108], milk powder, or bacteriological peptone [107] has a positive effect on fly longevity [106] and fecundity [107]. An experiment by Bertinetti et al. (2019) with no feed, drinking water, agar with sugar water, and a mixture of sugar, bacteriological peptone, and milk powder resulted in increased oviposition and egg weight with a protein availability of 2.5% and 9%, respectively, for the agar and milk diet. The adult longevity was less than 10 d without feeding. Giving water increased the longevity by 3 d in male and 2 d in female flies. The provision of agar or milk did not significantly change the longevity in males, whereas female longevity increased to 13 and 15 d, respectively [107]. The oviposition period was 10 d in the agar diet and 17 d in the milk-based diet. The total egg mass obtained in the no diet (532 mg FM) and water diet (~556 mg FM) were lower than in the agar (~931 mg FM) and milk (~1552 mg FM) treatments. The egg hatchability was ~82% and differed significantly from the other three treatments with approximately 75% [107]. Similar to Bertinetti et al. (2019), Nakamura et al. (2016) reported an adult life span of 9–11 d without feeding the flies. However, they observed a tremendously increased longevity of approximately 21 d for both males and females when provided water. The longevity increased to approximately 48 d in females and 73 d in males with a sugar diet [19]. Besides sugar and water, the life history traits of adults were examined by a feeding experiment with protein-rich (0.05–0.5%), carbohydrate-rich (5–50%), and a 0.5% saline solution [108]. Here, the feeding rate was 2 mL/pair/d of the corresponding solutions. The adult longevity was approximately 6 d with no feeding, 18–21 d with tap water, 16–19 d with distilled water, and 10–13 d with 0.5% NaCl. The females failed to lay eggs if they did not receive water. Feeding 5% honey increased the total egg yield to ~490 mg compared to ~321 mg in tap water, while 5% glucose led to a reduction of longevity (14 d) and egg yield (241 mg). When fed with the lowest concentrations of both microalgae powders, adult longevity decreased to 14–16 d, whereas the total egg yield did not differ compared to tap water [108].

It can be concluded that for higher adult longevity and egg mass, providing an energy source such as carbohydrates and protein is recommended rather than starving or offering only water at the adult stage.

3.8. Larval and Adult Density

It is important to ensure a consistent number of larvae per container depending on the amount of feed. The amount of feed one larva could consume varies between developmental stages (Figure 1b–f). The larvae have to be provided with enough feed to minimize intraspecific competition. However, too many larvae in a container can increase the substrate temperature to an uncomfortable level, which might result in larval escape and lower larval weight gain. The number of larvae used per unit area, and their stages as well as the container dimensions differ greatly between studies (Table 4). The lack of standardization makes the comparability of data considerably difficult.

Table 4. Density of BSF juveniles and adults in various studies.

BSF Density	Container Details	References
~0.03 larvae/cm^3	30 × 30 × 6.5 cm	[40]
~0.04 larvae/cm^3	76.5 × 56.5 × 30.5 cm	[24]
~0.08 larvae/cm^3	17.8 × 11.4 × 6.5 cm	[53]

Table 4. *Cont.*

BSF Density	Container Details	References
0.11 larvae/cm^3	21 × 27 × 16 cm	[2]
0.22 larvae/cm^3	60 × 40 × 30 cm	[79]
~0.11 larvae/cm^3	1.89 L	[82]
0.18 larvae/cm^3	5.5 L	[101]
0.2 larvae/cm^3	100 L	[82]
~1.7 larvae/cm^3	0.5 L	[22]
1.2 larvae/cm^2	-	[89]
1.45 larvae/cm^2	23 × 15 cm	[84]
2 larvae/cm^2	21 × 17 × 11 cm	[72]
6 larvae/cm^2	60 × 40 × 12 cm	[72]
2–6 larvae/cm^2	-	[43]
4.2 and 6.3 larvae/cm^2	~194–2060 cm^2	[109]
4–10 kg prepupae	1.0 × 1.0 × 2.5 m and 2.5 × 2.5 × 2.5 m	[110]
~111 flies/m^3	1.5 × 1.5 × 3.0 m	[111]
500–8500 flies/m^3	45 × 45 × 45 cm	[24]
740–3704 flies/m^3	30 × 30 × 30 cm	[112]
~741 flies/m^3	30 × 30 × 30 cm	[106]
~5080 flies/m^3	27 × 27 × 27 cm	[19]

Moreover, the age of inoculated larvae varies greatly. For example, Miranda et al. (2019) used neonates (<12 h after hatching), while other studies inoculated <1 d [53], 2 d [2], 3 d [17,99], 4 d [22,40], 5 d [45,72,78,94,113], 6 d [33,67], several day-old larvae [80,85,98,101,109,114] or even larvae older than 2 weeks after hatching [48]. It is only known that eggs and early instars are more fragile compared to later instars (Figure 1a–g) [17]. However, no recommendation on the ideal larval age for inoculation onto a feed is reported in the literature. In general, it can be stated that the influence of a feeding regime of interest is more difficult to trace with increasing age, as larvae may have been previously cultivated under different circumstances and diets.

Larval densities are reported either based on egg weight [15,63,91], larval numbers calculated based on the average weight of a given number of individuals [72,79,96], or by manually counting larvae [3,45,98]. Most publications only state the number of larvae or eggs that are inoculated onto the substrate [22,40] but not whether larvae were manually counted or weighed. When using eggs, the egg weights differed from 10 mg in 9.0 × 9.0 cm Petri dish containers [27] to 150–200 mg in 19.5 × 16.5 × 9.5 cm containers [15]. It is important to be aware of the differences in hatching rate depending on the egg clutches inoculated and the resulting stocking density.

Adult density and cage size are crucial variables because of their role in egg production [24,110]. The fly densities in various experiments ranged from ~111 [111] to 8500 [24] flies/m^3 in cages of different dimensions (Table 4). Based on the fly densities used for *M. domestica* [115], a density of ≥13,000 flies/m^3 is possible [24]. In a study examining densities of 500–8500 flies, the oviposition period was significantly shorter (11 d) at 500 flies/m^3 density compared to all the other densities (~15.9 d) [24]. The total egg mass obtained increased as the fly density per cage increased, i.e., 0.4 g at 500 flies/m^3 to 7.8 g at 8500 flies/m^3. The egg mass found in female-ratio-dominant cages was always higher but not significantly different for the densities of 500, 2500, and 4500 flies/m^3. In contrast, at 6500 flies/m^3 and 8500 flies/m^3, the egg mass collected from female-ratio-dominant cages was significantly higher (7.6 and 9.0 g) than the male-dominant cages (5.2 and 6.6 g), respectively. The egg hatching rate reduced although not significant from 97.5% at 500 flies/m^3 to 92.1% at 8500 flies/m^3. Authors recommend >6500 flies/m^3 in 45 × 45 × 45 cm cages [24]. The total number of eggs obtained (based on the egg weight of 100 eggs) were 8366, 20,772, and 42,633, respectively, for 740, 1852, and 3704 flies/m^3. The density of flies in this study did not affect adult survival [112]. According to Park et al. (2016), it is recommended to use higher densities of 8–10 kg prepupae in cages ranging between 1.0 × 1.0 × 2.5 m and

2.5 × 2.5 × 2.5 m to increase the number of eggs and their mass, instead of using lower densities (4 kg prepupae) [110].

It is hence noticeable that there is a considerable discrepancy between the studies, particularly in the implementation and information provided, and that no standard density of larvae or flies could be determined to achieve optimum yield.

3.9. Ambient Temperature and Relative Humidity

Ambient temperature is the temperature of the chamber or immediate environment, where the insects are reared at a relative humidity (RH) that is often controllable. The BSF thrive well in tropical climatic conditions at most of their life stages due to their habitat origin [116], which refers to rearing temperatures above 25 °C and a comparatively high RH. However, providing a tropical climate throughout the year in the northern hemisphere is expensive. That makes it important to know the exact conditions required at different life stages in BSF production. The ambient temperature for the larval stages corresponds to the substrate temperature (besides larval aggregation temperature) and hence most of it is mentioned in the substrate temperature chapter. In the case of other life stages, temperature is an essential variable as well. The range of temperatures tested or maintained for adult longevity, mating, oviposition, and egg hatchability was between 10 and 42 °C [20,73,88]. According to Holmes et al. (2016), at 12 °C (and 70% RH), eggs fail to hatch, while at 16 °C, the time taken for egg eclosion is 7 d longer than at 19 °C (approximately 8 d). Also, the eclosion rate at an ambient temperature of 16 °C was found to be only approximately 12% compared to 75% at 19 °C. The early instar larvae from the 16 °C ambient temperature died within 3 d. In the 19 °C conditions, the rate of adult emergence was approximately 32%, indicating that the minimum threshold temperature in rearing BSF is 19 °C [117]. The pre-oviposition time was as long as 16 d at 20 °C in contrast to just 5 d at 35 °C. However, the highest egg numbers were obtained at 30 °C. No oviposition was observed at temperatures less than 12 °C [21]. The egg viability was lower than 11% at 10, 37, 40, and 42 °C. The egg eclosion time was shorter as the temperature increased from 15 to 40 °C. The eclosion was 11.4 d faster at 35 °C than at 15 °C. The highest egg eclosion rates were at 30 and 35 °C with an average of 75% [88]. Another experiment with a temperature range of 20.5–39.8 °C observed up to 99.6% of the oviposition between the temperature ranges of 27.5–37.5 °C [20].

In general, temperatures of approximately 26–30 °C and 60–70% RH are maintained in the majority of publications. A RH of 59–82% was recorded during the bioconversion of feed by BSF larvae [45]. Holmes et al. (2012) studied a RH range between 25–70% for egg eclosion and adult emergence. The prepupal development took the longest (10.4 d) at 25% RH and shortest (9.5 d) at 70% RH. The pupal and adult mortality were 65, 23, and 2% and 84, 41, and 7%, respectively, for increasing RH of 25, 50 and 70%. The adult life span was shortest (~5 d) at 25% RH and longest (~8 d) at 70% RH [118]. Under high ambient temperatures, maintaining a higher RH range of 60–70% RH can minimize evaporation from eggs or moist feeding substrates. Up to 75% of eggs hatched in just 2.6 d at 35 °C ambient temperature and 70% RH. However, the larval development time at this temperature took 16 d, whereas the shortest larval developmental time of 13 d was achieved at 30 °C (70% RH) [88]. The extent to which RH affects larval growth performance is limited based on the few publications that focus on this factor.

The RH in different rearing setups and experiments includes a range of 25–90% for both flies and eggs. Jucker et al. (2017) maintained the flies at 25% RH [3]. According to Sheppard et al. (2002), mating and oviposition can be observed at a wide range of 30–90% RH [17]. There are no studies that explicitly examine the effect of varying RH on fly performance or egg hatching, except Holmes et al. (2012). Here, the egg eclosion was approximately 7, 20, 38, 73, and 38%, respectively, at a RH of 25, 40, 50, 60, and 70%. The time taken for egg eclosion was the longest (~131 d) at 25% RH in comparison to 71 d at 60% RH and 84 d at 70% RH [118]. An adequate RH is important to prevent egg desiccation; spraying water [75,119] or using wet tissues [21] are some of the commonly used techniques.

In particular, understanding the specifics of RH could facilitate the transport of live animals and improve the safety and efficiency of regular supplies of young larvae to small, decentralized insect farmers. Based on the results of the above-mentioned studies, an ambient temperature of approximately 28 °C and a RH of approximately 70% seems to be ideal for BSF production.

3.10. Light

Light, or photoperiod, is the number of hours in a day in which an organism receives illumination. Although the influence of photoperiod on BSF larvae is unknown, studies are maintaining specific photoperiods in larval rearing. The photoperiod tested ranges between zero [63,81,98], 10 h [107], 12 h [2,45,53,73,86,99], 14 h [22,76,117] and 16 h [27], or as natural sunlight through a greenhouse [82]. The egg hatching is not affected by light color temperature [120], nor by light intensity [24]. The photoperiod does not affect egg hatching as well [24]. Nevertheless, in some studies, eggs were light exposed for 12 h [118], 14 h [22,26,76,94], 16 h [27,52] to 24 h [39]. The reason for this is probably that the different developmental stages do not have to be spatially separated, thus saving money and space. The mating of BSF is most efficient under natural sunlight [111,121]. Illumination via artificial sources was shown to stimulate reproduction in adult BSF as well, offering a way for commercial year-round production [27,119,122,123]. For artificial illumination, various systems have been examined, including fluorescence lamps [106,119,122], quartz–iodine lamps [121], light-emitting diodes (LEDs, [106,119,122,123]), halogen lamps [119,122], and metal halide lamps [121]. The wavelengths studied were 300–885 nm [122], 332–535 nm [106], 350–450 nm and 350–2500 nm [121], 380–780 nm [24], and 400–700 nm [121] range. The light intensity range included 700–3700 lux [27], 3–800 μmol/m^2/s [111], 40 μmol/m^2/s [24], ~50–200 μmol/m^2/s [121], 59 μmol/m^2/s [119], and 300 μmol/m^2/s [108]. Liu et al. (2020) tested four artificial light sources for mating success and egg clutches. They used a 50 W halogen lamp, a combined white LED and compact fluorescent lamp of 50 W each, a 400 W metal halide lamp, and a 20 W LED lamp that matched the visual spectral sensitivity of adult BSF. From each light source, wavelengths of 300–885 nm were maintained. The highest mating success (90%) and proportion of fertile egg clutches (91.4%) were achieved from the 20 W LED lamp. No fertile egg clutches were found for the metal halide light [122]. A 500 W quartz-iodine lamp (350–2500 nm) and a 450 W rare-earth lamp (350–450 nm) were used to study mating and oviposition in BSF. The number of mating pairs observed was 70, 40, and zero for sunlight, quartz-iodine, and rare-earth lamp, respectively [121]. Artificial light rich in ~440–540 nm is recommended for enhanced mating [123]. Ultraviolet, blue, and green light between the wavelengths 332 and 535 nm are perceived by the BSF adults, influencing their mating behavior [106]. However, Zhang et al. (2010) suggest a wavelength spectrum of 450–700 nm. The mating peak was observed at an irradiance of 110 μmol/m^2/s [121]. Tomberlin and Sheppard (2002) recommend maintaining a minimum light intensity of 63 μmol/m^2/s, and, for optimum mating, an intensity of >200 μmol/m^2/s [111]. The mating rate increased from 23 to 70% as the irradiance increased from 0.92 W/m^2 to 431 W/m^2 [123]. The oviposition peak was on the 17th and 13th d for sunlight versus the quartz-iodine lamp and both took 4 d for egg hatching [121]. The day of oviposition was (~16 d) with a LED of low intensity (~14 W/m^2), whereas it was approximately 13, 11, and 10 d, respectively, for an LED of high intensity (~24 W/m^2), a fluorescent tube of low intensity (~5 W/m^2), and a fluorescent tube of high intensity (~23 W/m^2) [106]. Here, the authors conclude that the higher light intensity in the cages decreases longevity because of higher energy loss due to increased flying activity. LED illumination is considered to support a higher egg hatchability within the same number of egg clutches in comparison to fluorescent tubes [106].

The photoperiod differs between the studies and was shown to have an effect on fly performance. The oviposition period is light dependent [19,24,119,121]. The experimental or rearing photoperiod ranged between 2–16 h [19], 6–18 h [24], 8–16 h [112], 9 h [121], 10 h [107], 12 h [20,61,88,106,109], 14 h [93], 15 h [73], and 16 h [119]. According to Hoc et al. (2019), the illumination periods of 2–6 h and 12–18 h had oviposition peaks at 5 and 3 d,

respectively. The lowest light duration in this study yielded the lowest egg mass (4.1 g). Although the egg hatching was not influenced by photoperiod, increasing light duration from 6 to 18 h reduced the oviposition period by 3 d [24].

Neither egg hatching, nor the development of juvenile stages of BSF has been shown to be affected by light exposure, thus saving energy. In contrast, different variables of lighting, including wavelength spectrum, photoperiod, intensity, and color temperature are crucial modulators for reproductive success.

4. Assessment of BSF Larvae on Various Feeding Substrates

Although BSF larvae are popularly known as voracious feeders of biodegradable substances, their performance in terms of survival rate, developmental time, biomass, and capacity to reduce waste differs depending on the nutritional composition of the substrate. The compilation of larval growth and development on various biodegradable materials helps to obtain an overall picture of what could be more suitable for the larvae and how they can be used as converters of biodegradable substances based on their specific needs. Although the current EU regulations restrict the use of certain side streams as feed, there is a huge potential in utilizing available side streams of animal or plant origin. These include livestock side streams such as manure, slaughterhouse waste, dairy side streams, as well as food waste or agricultural side streams consisting of vegetable and fruit production and processing side streams, seed press cakes, brewer's grain, fisheries side streams, and seed husks.

The comprehensive chapter on manure is intended to provide insight into its use as feed for BSF larvae. Other agricultural side streams and food wastes could be fed to other livestock animals [124] but manure remains unused except for its use as compost or fertilizer. Therefore, the use of manure as feed for BSF larvae can minimize the competition between different animals for feed availability. Hence, a compilation of manure studies on BSF performance is gathered in the next chapter. In addition, aquaculture (and fisheries) side streams like fish rendering and fish offal, meat and bone meal, feathers, and bedding materials are also categorized as side streams. These can be a potential source of feed for the insects.

4.1. Manure

BSF larvae are found to thrive on different manure-based substrates [40,67]. Among the feed trials on manure, the ones that are used widely are chicken manure, pig manure, and cow manure. The properties of manure seem to influence larval survival. Miranda et al. (2019) found that the BSF pupation rate was 60–80% higher in fresh chicken manure compared to 2 and 4 d aged chicken manure. In this experiment, the pupation was not observed when the BSF larvae were added to the 6 and 8 d old manure [103].

In general, feed trials sometimes include manure with additives, such as specific microbes or chabazite, a zeolite that reduces unpleasant odor by absorbing volatile compounds such as ammonia (Table 5). It can be summarized that on chicken manure survival of larvae becomes challenging if the substrate moisture is too high or if the manure is aged. The larval development time is predominantly longer when feeding manure in comparison to high-quality standard diets, as shown by Oonincx et al. (2015), where the development took 20 d on a chicken feed diet [53]. In addition, the developmental time to reach the prepupal stage in fresh chicken manure was shorter (16 d; [103]). This discrepancy could be explained either by the drying and remoistening process [53] or changes in the manure-associated microbial community and changes in the nutritional composition due to the ongoing degradation process. In most cases, larvae need approximately 20–25 d of developmental time on fresh chicken manure.

Table 5. Survival rate (%), developmental duration (d), and individual BSF weight (mg FM) on chicken manure-based diets.

Feed	Survival Rate (%)	Duration (d)	BSF Stage	BSF Weight (mg FM)	References
ChM (air-dried and remoistened to 80–90%)	0.0	NA	Larva	NA	[50]
ChM (dried and remoistened to ~66%)	82.0	144	Larva	57.0	[53]
ChM + chabazite + water	86.0	-	Prepupa	90.0	[125]
ChM + *B. subtilis* strain S19	99.3	-	Prepupa	87.0	[68]
ChM + *B. subtilis* strain S15	98.7	-	Prepupa	95.0	[68]
ChM (frozen and thawed)	98.0	-	Prepupa	78.0	[68]
ChM: Cow manure 3:2	95.0	21	Larva	90.5	[67]
ChM: Cow manure 3:2 + *Bacillus* sp. strain MRO_2	99.1	19	Larva	112.5	[67]
ChM (fresh)	-	26	Prepupa	225.0	[113]
ChM (fresh)	-	13	Larva	80.0	[69]
ChM (fresh) + *B. subtilis* strain BSF-CL	-	13	Larva	93.0	[69]

ChM—chicken manure.

The larval weight was 116 mg FM in chicken feed but only 57, 69, and 74 mg FM in chicken, pig, and cow manure, respectively. Here it should be noted that the provided feed amount was rather low (60 mg/larva). The larvae were harvested when the first prepupa was observed [53]. The use of fresh poultry manure resulted in the prepupae weighing almost 225 mg FM [113]. In contrast, the prepupae weight in the fresh chicken manure was only 53 mg FM [103]. The larvae of 93 mg FM were obtained on chicken manure and inoculated with the *Bacillus subtilis* strain BSF-CL at 1×10^9 CFU/mL (1 L of bacterial inoculation to 1000 kg manure). Without bacterial inoculation, the weight of the larva was only 80 mg FM [69]. Chicken manure yielded higher larval mass in 14 d when inoculated with *Kocurina marina*, *Proteus mirabilis*, and *Bacillus subtilis* (each had 22 mg DM) in comparison to the chicken manure without any inoculation (18 mg DM). In this study, the bacterial strains were inoculated at 1% (*v*/*w*) proportion onto 500 g chicken manure at a concentration of 1×10^8 CFU/mL [126]. These data show that microbes considered for a co-digestion process seem to be beneficial for BSF larvae (Table 5). Furthermore, BSF larvae are capable of reducing the bacterial load of manure-based substrates, as shown by Erickson et al. (2004) [85]. Here, the concentration of inoculated *E. coli* O157:H7 (10^7 CFU/g) in chicken manure was reduced to approximately 10^1 CFU/g within 3 d [85]. In contrast, no reduction of *Enterococcus* spp. was reported throughout the rearing cycle [85,127,128]. Larvae exposed to contaminated manure still contained viable *Salmonella enterica* Serovar Enteritidis after 6 d in their gut [85]. In addition, foodborne pathogens like *Bacillus cereus* could also be found in the BSF larval gut. This emphasizes proper decontamination before use as food or feed [129].

Sheppard et al. (1994) found a substrate reduction rate of up to 50% in their chicken manure management system. The amount of manure used is not specified by the authors [29]. In other studies, a total reduction rate of 75% of 300 g chicken manure [125], 35.8% of 1000 kg chicken manure [69], and 40.5% from 1000 kg chicken manure inoculated with the *Bacillus subtilis* strain BSF-CL were found [69]. The substrate reduction rate was better (54%) in *Bacillus subtilis*-inoculated chicken manure than in the control diet (49%) without bacterial inoculation [126]. Another study with *Bacillus* sp. strain MRO_2 inoculation had comparable results of 48% waste reduction from a chicken and dairy manure mix, whereas the control diet without bacterial inoculation was reduced by 42% [67].

These results indicate that the chicken manure can be managed very well using BSF. However, the substrate moisture, manure age, microbiome, and quality are some of the factors to be considered. Interestingly, no study so far highlights the effect of inoculating helpful microbes on the pathogens present in the manure.

The other widely tested manure is cow manure. The weight of larvae reared on cow manure and cow manure-based diet varies greatly (Table 6).

Table 6. Survival rate (%), developmental duration (d), stage of harvest, individual BSF weight (mg FM), and feeding rate on cow manure-based diets.

Feed	Survival Rate (%)	Duration (d)	BSF Stage	BSF Weight (mg FM)	Feeding Rate (mg FM/larva)	References
CoM	85.0	-	Prepupa	137	133	[52]
CoM	71.0	-	Prepupa	179	233	[52]
CoM	91.0	24	Larva	63	1000 [1]	[130]
CoM: SCR 1:4	98.8	21	Larva	123	1000 [1]	[130]
CoM: SCR 2:3	98.5	21	Larva	117	1000 [1]	[130]
CoM: SCR 3:2	98.4	21	Larva	112	1000 [1]	[130]
CoM (dried and remoistened)	87.8	214	Larva	~74	60	[53]
CoM	-	21	Prepupa	100	150	[36]
CoM: FO 9:1	-	21	Prepupa	140	150	[36]
CoM: FO 1:1	-	21	Prepupa	150	150	[36]

CoM—Cow manure; SCR—Soybean curd residue; FO—Fish offal. [1] Feeding rate in mg FM/larva/d.

The substrate reduction in cow manure was 26% [130] and 22% [96] on a dry matter basis. The percent waste reduction increased as the soybean curd residue replaced the cow manure [130]. According to the authors, BSF larvae reared on cow manure can be used to produce clean energy coupled with manure management since they produced approximately 16 g of BSF oil in 10 d from 1200 larvae [96]. In cow manure, the *E. coli* O157:H7 abundance was similar (~10^7 CFU/g) with or without larvae and at all three temperatures and feed regimes examined [85]. Contrastingly, the presence of 15 d old BSF larvae significantly reduced the *E. coli* O157:H7 concentration in cow manure from approximately 10^7 CFU/g to 10^1 CFU/g in 3 d [127].

Pig manure was also a preferred substrate in the BSF larvae feed trials. Larvae of all ages were observed to prefer pig manure over a plant-based side stream diet, irrespective of the feed they were previously fed with. The preference for pig manure increased as the larval age increased. Admittedly, this study only conducted a preference behavior but information regarding larval development was not examined [98]. The larval survival rate was 97% in dried and remoistened pig manure with a developmental time of 144 d [53]. A study conducted by El-Dakar et al. (2021) harvested larvae of approximately 202 mg FM from fresh pig manure in 36 d of development [113]. In contrast, Veldkamp et al. (2021) yielded larvae weighing just 37 mg FM at the time of harvest, when 10% prepupae were formed. The lower weights could be due to the use of 7 d old manure in the experiment, which was stored at 4 °C until use. Additionally, some general rearing issues might explain the lower weight obtained for all dietary groups including the chicken feed control (69 mg FM) [104]. The *E. coli* O157:H7 population increased slightly in the presence of larvae in the pig manure unlike in chicken manure. However, the total biomass obtained was still higher (11 g) in pig manure than in chicken manure (5 g) [85]. In the manure management experiment using BSF, the on-farm reduction in pig manure mass was 56% DM in 14 d [54]. The waste reduction index for pig manure was 3 g DM/d [104].

The larval performance on manures from the same animal species might differ based on the feed and health condition of that particular animal. The variations in survival rate, growth, and development of BSF larvae fed similar substrates could be due to the different experimental setups, including manure age and storage, BSF strains used, time to harvest, feeding rates, and general differences in rearing conditions. More research is necessary on the use of manure and its effects not only on larval performance but also on its further use as an animal feed with a standardized rearing protocol [131]. For example, varying factors such as the initial larval age, experimental duration, climatic conditions, and stage of harvest do not give a comparable larval yield even on a similar substrate. A publication by Bosch et al. (2019), which proposes a protocol for conducting a feed trial for larval production can be used as a template. They suggest using a standard

rearing diet in addition to experimental diets [131]. There is no standardization protocol for trials with adults or parameter-specific studies on the BSF. However, providing detailed information on the experiment could help understand any existing differences in the results. Since manure is considered to have a high microbial load and studies postulate ambivalent data on pathogen reduction or accumulation after BSF treatment, further experiments are recommended. However, high larval survival rates indicate a species-appropriate rearing when manure is used as feed.

4.2. Food Waste and Agriculture Side Streams

Food wastes and agricultural side streams encompass kitchen, household, canteen, and restaurant leftovers, vegetable and fruit scraps, as well as side streams from plant- and animal-based industries. Generally, these side streams are highly heterogeneous making it hard to standardize a consistent composition. At times, this could include leftovers of both plant and animal origin. Many experiments considered food waste either in whole or in combination as a feeding substrate for BSF larvae. Food processing wastes comprise the low-value side streams from agroindustry. The most popular feed trials with food waste and agricultural side streams are brewer's spent grain, fruit pomace, seed husk, soybean side streams, spent coffee, pressed seed cakes, bread and cookie remains, fermented empty fruit bunches and corn straw, potato peels, cassava peels, etc.

On kitchen waste, the survival rate of BSF larvae was only 41% [39]. Although not very different, on canteen food waste the survival rate until the pupae stage was up to 80%. However, when larvae were fed purely on oil waste from the canteen, the whole population failed to reach the pupae stage. The inhibited mobility and respiration due to the viscous consistency of oil waste and lack of easily digestible nutrients is a plausible reason for the lower survival rate and biomass increase [89]. On agricultural side streams and side streams from the food industry, the larval survival rates were above 90% such as for apple pulp, brewer's spent grain, corn meal, chicory roots, and fruit puree. None of the larvae survived on tomato leaves [132]. Feeding rice straw at 12.5 mg FM/larva/d was found to result in only half of the larvae surviving. In contrast, up to 92% and 98% survived for the feeding rates of 100 mg FM/larva/d and 200 mg FM/larva/d, respectively [32]. That implies the possibility of overfeeding low-value substrates as the larvae are able to extract the required nutrients. The brewer's spent grain obtained from four different companies was formulated by either adding just water, brewer's yeast, or molasses. This resulted in a total of twelve different diet formulations. The diets significantly differed in their macronutrient contents but the survival rate was $\geq$85% for all treatments [105]. On spent coffee, sweet potato, and dough the survival rates were 98, 87, and 83%, respectively [133]. On cottonseed press cake, the survival rate was >99%. This suggests that the presence of anti-nutritional diet components like gossypol did not negatively affect the survival rate [75]. On fish-rendering products, the larval survival rate was just 1.5%. The possible heavy metal contents in the fish diet are considered to be detrimental to larval growth by the authors [39]. A survival rate of 89% was found on food waste with a fat content of 12% [132]. Similarly, the crude fat contents of approximately 9, 13, and 19% for vegetables, tofu side streams, and food waste diet had no hindrance on larval performance. For example, larvae weighed 179, 200, and 193 mg FM, respectively, when reared for 14 d on vegetables, tofu side streams, and food wastes [91]. Although larvae can survive on most diets, several factors and diet characteristics listed in this review affect the life history traits of larvae considerably. In addition, even if the larvae manage to stay alive the time taken for development is highly variable. On a rice straw diet at a 200 mg FM/larva/d feeding rate, the larvae reached the prepupal stage in 38 d, while lower feeding rates like 12.5 mg FM/larva/d extended the larval developmental time to 54 d [32]. At a 100 mg FM/larva/d feeding rate, the larval development time was ~25 d on diets consisting of vegetable wastes or tofu dreg [31]. The total developmental time to reach the pupal stage was 22 d on a food waste diet [89]. A developmental time of 31 d was taken on brewer's spent grain consisting of a sorghum–barley–water mix to reach the pupal stage. A development time of ~26 d was found in

three diet formulations composed of malt–barley–water, sorghum–barley–brewer's yeast, and barley–water diet mixes [105].

Larval weight is an important factor in choosing the diet mixture. The larval weights varied between 3 and 226 mg FM when fed on various food wastes and agricultural side streams. On kitchen waste and fruit and vegetable wastes, the larval weight was 173 mg and 123 mg FM, respectively [39]. Another study by Nguyen and colleagues (2015) obtained a larval weight of 226 mg FM on kitchen waste. The reason could be the difference in fat content [40]. In the former kitchen waste, the fat content of the diet was only approximately 5% and, in the latter, 20%. In addition, the fat:protein ratio, as well as the amino acid and fatty acid profile, might play a role [134]. The high protein and high-fat diet obtained by mixing agricultural side streams gave an 86% survival rate in comparison to a low-protein and high-fat diet (72%) until observing the first prepupa [41]. The prepupal weight on a rice straw diet at a 200 mg FM/larva/d feeding rate was only 13.6 mg DM in 38 d [32]. Another study on rice straw resulted in 100% inhibition of larval growth [61]. The addition of restaurant wastes to rice straw by an 80:20 ratio resulted in a larval weight of approximately 49 mg DM; harvested at the 50% prepupae stage. Based on additional optimization tests, restaurant solid waste and rice straw mix represented 70:30 and 0.35% of Rid-X, a commercial product with functional microbes and enzymes able to break down cellulose, lipids, and proteins, leading to a larval weight of approximately 61 mg DM [33]. The larvae reared on solid residual fraction, a residue produced after oil extraction from restaurant waste, weighed 65 mg FM [55]. Industrial food waste and household food waste yielded final larval weights of approximately 176 mg and 65 mg FM within 9 d, respectively [132]. The unexpected low larval weight of 65 mg FM on household waste cannot be explained by the nutritional quality of the diet. However, the possible presence of some harmful substances (pesticides, cleaning chemicals, etc.) might have inhibited larval growth [132]. Although the survival rate in apple pulp was up to 95.5%, the larval weight was just ~38 mg FM. It was postulated that the combination of a pH of 3.7, lower protein content (3.4%), high crude fiber (25.7%), and cellulose (21.5%) in apple pulp inhibits larval growth. Similarly, feeding fruit puree led to lower larval weights (80 mg FM) even with a 99% survival rate [132]. Fiber-rich palm oil side streams used by Klüber et al. (2022), yielded larvae of 187 mg FM in a *Bjerkandera adusta* fermented diet in ~30 d in comparison to ~149 mg FM in a non-fermented reference diet in ~41 d. The chicken feed diet in the same experiment yielded larvae of 303 mg FM in ~22 d [63]. Chia et al. (2018) prepared 12 different diets from brewer's spent grain (sorghum, barley), brewer's yeast, and cane molasses, and the best results were obtained from the following diet mixes. The larval weight in the sorghum–barley–water diet mix was ~150 mg FM, while ~200 mg FM was yielded from a barley–water diet mix. Larvae of similar weights (~150–200 mg FM) were harvested from barley–brewer's yeast, malt–barley–brewer's yeast–molasses, and sorghum–barley–brewer's yeast–molasses diet mixes. Larvae were collected as soon as they developed into pupae [105]. Composted cocoa pod husks in combination with food waste resulted in a larval weight of 112 mg FM within 18 d. The prepupal weight of 150 mg FM was obtained from larvae fed on tofu dreg [31]. The larval weight on the cottonseed press cake was approximately 160 mg FM [75]. The individual weight based on the biomass harvested was 165 mg FM in the apple and spent grain diet. A slightly lower weight of 145 mg FM was found on a diet consisting of spent grain and banana. The use of pure fruits drastically reduced the larval weight to 88–105 mg FM for banana, apple, and a mixture thereof, in comparison to spent grain alone with 136 mg FM [135]. Larval weights were 22 mg, 164 mg, and 171 mg FM on oil waste, food waste, and chicken feed, respectively [89]. On fish render, larvae gained 143 mg FM [39] and 167 mg FM [40]. The lower larval weight in fish renders in comparison to kitchen waste (173 mg FM) could be caused by the bioaccumulation of heavy metals.

The use of organic wastes as feed for larvae also aims at a reduction in substrate volume. Substrate reduction after the larval harvest has been measured in some experiments. A substrate reduction of up to 85% was observed for canteen food waste. The percent substrate reduction was 66 and 2.4% on chicken feed and oil waste, respectively [89].

Brewer's grain and corn meal had a similar waste reduction percentage of approximately 45%. Industrial food waste had a substrate degradation of 59%. Apple pulp and household food waste had approximately an 18% substrate reduction [132]. The substrate reduction was 79% for the fruits and vegetable diet, followed by 70% for bakery, 64% for cheese, 61% for sugar beet waste, and approximately 52% for brewer's grain and yeast [37]. The percentage of substrate reduction was 74% for the apple–spent grain substrate mix. A substrate degradation of 59% was found in an apple–banana diet mix [134].

It is evident that BSF larvae are capable of thriving on various organic substrates. However, the results of these feeding studies emphasize the complexity of the larval feeding regime, particularly the availability and ratio of required nutrients, the absence of contaminants, and the provision of appropriate amounts of feed. Moreover, differences in larvae performance could be attributed to dissimilarities in rearing conditions and substrate properties in terms of particle size, and substrate moisture among other factors. The distinguishable experimental approaches by the researchers have to be standardized or at least kept in mind to make an unbiased comparison of results.

5. Conclusions

For an optimized and sustainable production of BSF as a source of food and feed, ample research on available side streams and appropriate rearing conditions is crucial. Although the earlier studies conducted on BSF rearing provide good information on their performances, it is clear that the protocols and approaches in measuring the listed rearing variables differed tremendously. These differences make it challenging to compare the results between studies but even harder to translate knowledge to an industrial application. Here, a comprehensive overview of biotic and abiotic variables to be kept in mind is highlighted. These include substrate chosen as feed and its properties, environmental conditions, and container or cage type to facilitate optimum circumstances for BSF growth and development.

According to the studies analyzed, the mortality rate of larvae grown on agricultural side streams is relatively low while their performances differ between the diets, which is promising. Combining different side streams in a way that their nutritional profiles complement each other could compensate individual deficiencies. In consequence, low-value agricultural side streams can be adjusted to the nutritional requirements of BSF larvae, creating a sustainable feeding system that contributes to a circular economy. In addition, this review also guides define the range of variables to be tested in the future; ensuring an improvement first in research and long-term for BSF production.

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