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Metabolic Engineering and Synthetic Biology – Review

Extrapolation of design strategies for lignocellulosic biomass conversion to the challenge of plastic waste

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Abstract: The goal of cost-effective production of fuels and chemicals from biomass has been a substantial driver of the development of the field of metabolic engineering. The resulting design principles and procedures provide a guide for the development of cost-effective methods for degradation, and possibly even valorization, of plastic wastes. Here, we highlight these parallels, using the creative work of Lonnie O'Neal (Neal) Ingram in enabling production of fuels and chemicals from lignocellulosic biomass, with a focus on ethanol production as an exemplar process.

Keywords: Plastic valorization, plastic degradation, process design, metabolic engineering, hybrid processing

Introduction

The invention of vulcanized rubber in 1893 opened the doors for the development of synthetic polymers (Barker, 1940). The versatility in polymer types and blends allows diverse applications ranging from household goods to medical equipment and single-use supplies (Andrady & Neal, 2009). Currently, most plastic polymers are derived from petrochemicals in processes designed to produce stable, durable materials. This stability to various abiotic and biotic processes results in the accumulation of synthetic plastic polymers in the environment, including microplastics (Sharma & Chatterjee, 2017). The global production of plastic continues to increase (Elhacham et al., 2020) and much of this plastic waste ends up in landfills and water bodies (Law et al., 2020). Various studies have shown that approximately 80 wt% of the debris collected from the ocean floor is plastic (Selvam et al., 2021). Thus, there is a need for the development of processes that reuse, recycle or repurpose these materials (Lau et al., 2020).

Here, we focus on biologically mediated repurposing of these materials (Fig. 1). Ongoing efforts to improve chemical and thermal-based processes are described elsewhere (Liu et al., 2021; Monsigny et al., 2018; Padhan & Sreeram, 2019; Qureshi et al., 2020; Rahimi & Garcia, 2017; Vollmer et al., 2020). It has also been demonstrated that plastic monomers traditionally derived from petroleum can be produced by engineered microbes (Karp et al., 2017) and plants (Hillmyer, 2017; Rasutis et al., 2015).

The environmental accumulation of carbon-rich plastics due to an insufficient biological sink is reminiscent of the carbonaceous period in which lignin production drastically outpaced its biodegradation, and much of this lignin still exists in the form of coal and shale oil deposits (Robinson, 1990). This leads to the intriguing premise that petroleum-derived plastics are ultimately derived from lignin and this novel biological functionality that arose 300 million years ago is still wreaking havoc, but this question is beyond the scope of this review. Persistence of lignocellulosic biomass in the environment is no longer a problem and it is actually an appealing source of carbon and energy for the microbial production of fuels and chemicals. The continued progress in the engineering of microbes for utilization and valorization of biomass makes them a tantalizing candidate for addressing the plastic waste problem.

The challenges of developing microbial cell factories that can degrade, or even valorize plastic waste in an economically viable process parallels the challenge of developing microbial cell factories for the valorization of lignocellulosic biomass (Fig. 2). The topic of microbial degradation, and possibly valorization, of plastic waste has been repeatedly reviewed elsewhere, as described below. Here, we highlight the parallels between plastic utilization and biomass utilization, with a focus on Lonnie O. Ingram's extensive body of work related to biomass valorization.

Biomass and Plastic Waste Are Both Heterogenous

Biomass Composition

In contrast to virgin plastics, biomass is inherently heterogeneous. The three major components of lignocellulosic biomass are cellulose, hemicellulose and lignin. Cellulose and hemicellulose are biological polymers, each consisting of repeating monomeric units of hexose and pentose sugars, respectively. Lignin is a heteropolymer of the phenylpropanoid monomers guaiacyl (G type), syringyl (S type), and p-hydroxyphenyl (H type) (Davis et al., 2016). Biomass also contains less abundant metabolic components, such as nucleic acids, proteins, pigments and waxes, referred to in some contexts as non-structural components or extractives (Airoldi et al., 2019; de Araujo Silva et al., 2021; Horhammer et al., 2018).

Biomass composition varies substantially according to species (Chi et al., 2019), but is also impacted by growth conditions (Dennison et al., 2019; Templeton et al., 2009) and storage conditions (Smith et al., 2020; Towey et al., 2019; Wendt & Zhao, 2020) of the harvested biomass. Similar to the challenge of contaminants in mixed plastic wastes, harvested biomass often contains sand and soil, the presence of which can negatively impact biomass

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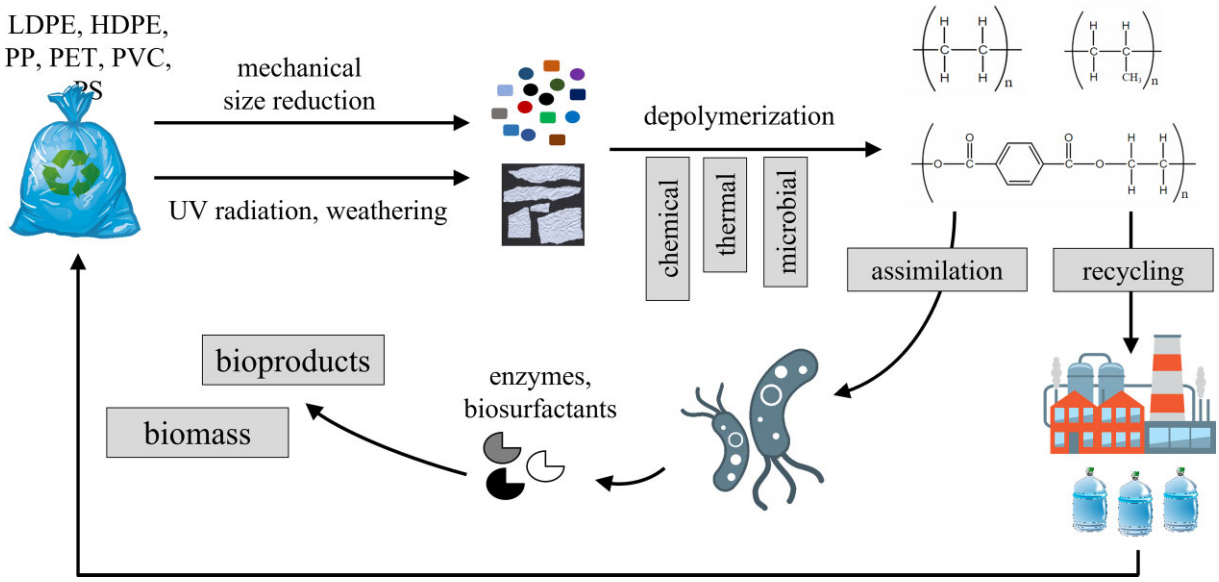

Fig. 1. Overview of possible means of plastic degradation and valorization.

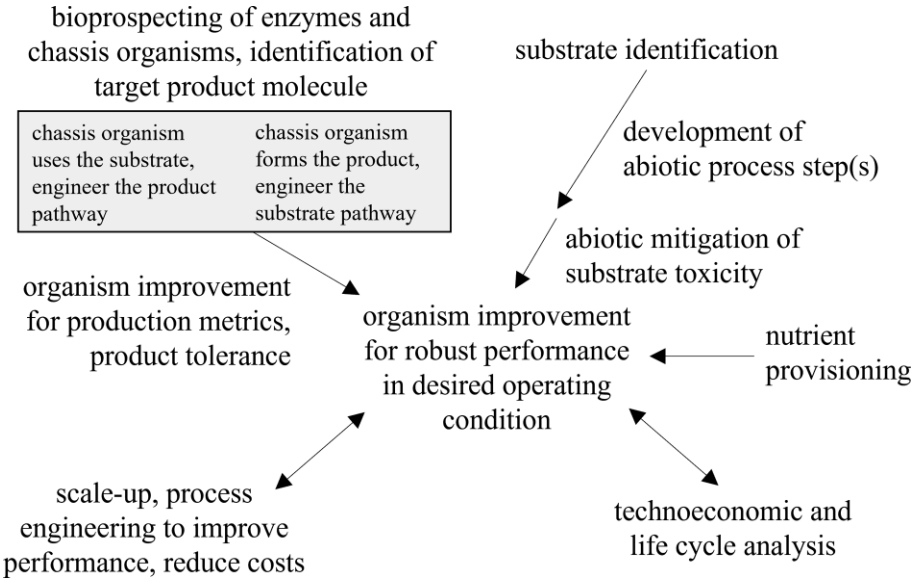

Fig. 2. Summary of the overall process design procedure.

hydrolysis, often requiring the addition of a process step for their removal (Horhammer et al., 2018).

Plastic Composition

Some of the common polymers in plastic waste include polyethylene (PE), polyethylene terephthalate (PET), polyvinylchloride (PVC), polypropylene (PP) and polystyrene (PS). Any process that aims to degrade or valorize plastic waste needs to be capable not only of utilizing the polymeric materials, but it must also be robust to the heterogenous nature of plastic waste, both in terms of the type of plastic, but also the presence of various impurities. Commercially available flakes of recycled PP were found to contain roughly 4% PE and 1–4% of a combination of PET, PS and PVC, as well as small amounts of textiles, aluminum and paper (Alvarado Charcon et al., 2020). The same analysis determined that recycled PE flakes contained roughly 5% PP and 1–4% other plastics.

PE is produced as either high-density polyethylene (HDPE) or low-density polyethylene (LDPE) and is used in plastic bottles, shopping bags, packaging, toys and household items (Andrady & Neal, 2009; Rahimi & Garcia, 2017). LDPE's recalcitrance to degradation is demonstrated by the fact that it took more than 30 years for a buried PE sheet to attain measurable levels of degradation and weight reduction (Otake et al., 1995). PET's backbone linkage of ester bonds provides high stability (Kawai et al., 2019; Liu et al., 2019). It is a strong and durable semi-crystalline thermoplastic polyester representing almost 50% of the world's synthetic fiber production (Crippa & Morico, 2020). PET has been used for the production of beverage containers, electronics and textile fibers (Webb et al., 2013). PET is commonly reused rather than

recycling, and with every use, the quality of polymer degrades. PVC is commonly used in the production of bottles, shoe soles, pipes and plastic cards. PP is a polymer of repeating units of propane-1,2-diyl, with applications in packaging, and medical, industrial and domestic utilization (Arutchelvi et al., 2008; Shah et al., 2008). PS is used not only in the packaging industry but also in daily consumables.

In addition to the plastic polymer, plastic often contains additives (such as dyes). Mixed plastic waste often contains other components (such as silica and glass), residual food and dirt (Andrady & Neal, 2009). Some of this material can be removed with a pretreatment step such as washing, though these contribute to the overall process cost. Plastics have been repeatedly described as comprising roughly 10% of household waste (Mathioudakis et al., 2021; Noufal et al., 2020; Zhou et al., 2014). In European municipal solid waste, PE (HDPE and LDPE) was the most abundant plastic, followed by PP, PET and PS (Dahlbo et al., 2018; Moellnitz et al., 2020). Commercial waste contained less PP than municipal waste, but all other polymers were roughly equivalent (author's own calculations from Moellnitz et al., (2020)). One study found that European commercial and municipal waste each contain roughly 1% PVC and PS, and 2% PP, with commercial waste containing 8% PE and municipal waste containing 5% PE (author's own calculations from Moellnitz et al., (2020)). Plastic waste from the western North Atlantic Ocean appeared to be highly enriched for HDPE, with some LDPE and PP, while the corresponding beach waste consisted mainly of PP and LDPE, with some HDPE, PS, PV and PET (Moret-Ferguson et al., 2010).

Direct Biological Utilization of Biomass and Plastic

Biomass

The fact that cellulose is a polymer of the hexose sugars generally preferred by microbes has motivated extensive work with cellulolytic organisms and cellulase enzymes. In the context of microbial cell factories, there are two general options for biological depolymerization of cellulose: use of an organism that is capable of producing its own cellulase enzymes, or exogenous provisioning of cellulase enzymes that were either purchased or produced in a distinct process step. Commercially available cellulase enzymes have often been subjected to extensive protein engineering to improve performance metrics (Chandel et al., 2012).

Microbial species that are inherently cellulolytic often require genetic modification to achieve production of the desired target molecule. For example, metabolic engineering of cellulolytic *Caldicellulosiruptor bescii* for expression of the ethanol production pathway resulted in the conversion of filter paper (cellulose) and switchgrass to ethanol (Chung et al., 2014). The Ingram group engineered two species with inherent cellobiose depolymerization capacity for the production of ethanol: the soft-rot bacteria *Erwinia* (Beall & Ingram, 1993) and the soil bacteria *Klebsiella oxytoca*, abundant in cellulosic waste streams (Doran et al., 1994).

A parallel approach is to modify the production organism so that it is able to depolymerize cellulose and its subunits (Davison et al., 2020). The Ingram group used several iterations of this approach. *Escherichia coli* strains that had previously been engineered for ethanol production were further modified to express cellobiose phosphotransferase from *Bacillus stearothermophilus* (Lai & Ingram, 1993), cellobiose-depolymerization enzymes from *K. oxytoca* (Moniruzzaman et al., 1997), and endoglucanase enzymes from *Erwinia chrysanthemi* (Wood, Beall, et al., 1997; Zhou et al., 1999). As described above, *K. oxytoca* was engineered for ethanol production. The native cellobiose-depolymerization activity of this organism was expanded by expression of cellulase from *Clostridium thermocellum* (Wood & Ingram, 1992), and *E. chrysanthemi* endoglucanase (Zhou & Ingram, 1999; Zhou & Ingram, 2001). Ultimately, the Ingram group shifted to the use of abiotic biomass depolymerization in conjunction with commercial enzyme supplementation, as described below.

The pentose sugars comprising hemicellulose are generally less preferred by microbes relative to hexose sugars, and yet valorization of these molecules is key to the economic viability of a biorefinery. The Ingram group used a grass-fed anaerobic digester as a source of potential hemicellulose depolymerization enzymes, resulting in identification of *Butyrivibrio fibrisolvens* isolates with the ability to use xylan (hemicellulose) as the sole carbon source (Sewell et al., 1988). Subsequently, *E. coli* and *K. oxytoca* engineered to produce ethanol were further modified to express the *C. thermocellum* xylanase enzyme (Burchhardt & Ingram, 1992). Ethanologenic *E. coli* was eventually modified to express the xylodextrin enzymes from *K. oxytoca* (Qian et al., 2003).

The Ingram group extensively used evolutionary methods for organism improvement. A hallmark of this work is the direct linkage of growth of the organism and production of the desired molecule. For example, the central metabolism of *E. coli* was modified such that the only way for the cells to maintain redox balance was through the ethanol production pathway (Ohta et al., 1991; Yomano et al., 2008). In this manner, cells with mutations that supported ethanol production were able to grow faster than other cells. Similar strategies were used for production of lactic acid (Grabar et al., 2006; Zhou et al., 2006; Zhou et al., 2005; Zhou et al., 2003), alanine (Zhang et al., 2007) and succinate (Jantama et al., 2008a; Jantama et al., 2008b; Zhang et al., 2009a; Zhang et al., 2009b). *E. coli* strain KO11, evolved for ethanol production, was subjected to genome analysis by optical (whole-genome) mapping, resulting in identification of extensive genetic duplication of the ethanol production cassette, as well as large-scale rearrangements of the chromosome (Turner et al., 2012). This type of structural chromosomal analysis remains relatively unusual in analysis of bacterial genomes (Yuan et al., 2020), as opposed to next-generation sequencing (Cao et al., 2020).

Lignin is a heteropolymer consisting of aromatic monomers (Davis et al., 2016). Direct biological utilization of lignin is unusual; processes that involve some sort of pretreatment are described below. While the polysaccharide pectin is often overlooked as a biomass component, it makes up a substantial fraction of some agricultural residues, such as beet pulp (Martins et al., 2020). The Ingram group observed that an ethanologenic *E. coli* strain was able to robustly utilize the pectin component galacturonic acid (Grohmann et al., 1994). One of the Ingram groups' ethanologenic *E. coli* strains was modified for pectinolytic activity by the expression of select genes from *E. chrysanthemi* (Edwards et al., 2011).

Plastic

The analogous nature of enzymatic degradation of biomass and plastic has been previously noted (Chen et al., 2020). One can envision that development of industrial organisms for plastic degradation or valorization will follow the same basic path as that used for biomass utilization, particularly cellulose. Specifically, biological depolymerization of plastic will either be performed by an engineered organism or by exogenous provisioning of enzymes that were either purchased or produced in a distinct process step. There are many recent reviews describing microbial activity on plastics (Danso et al., 2019; Devi et al., 2016; Gautam et al., 2007;

Table 1. Microorganisms associated with plastic polymer degradation

Organism	Isolation site	Observed weight loss	Reference
Pseudomonas fluorescens	Plant root nodules	2% for HDPE, 90 days	Baculi et al. (2017)
Serratia marcescens		8% for HDPE, 90 days	
Bacillus cereus	Mixed waste dump site	35% for PE, 112 days	Muhonja et al. (2018)
Bacillus safensis		20% for PE, 112 days	
Bacillus amyloliquefaciens	Municipal solid waste	16% for LDPE, 60 days	Das & Kumar (2015)
Aspergillus clavatus JASK1	Landfill soil	20% for LDPE, 90 days	Gajendiran et al. (2016)
Stenotrophomonas sp. P2	Landfill waste plastic	8% for LDPE, 100 days	Dey et al. (2020)
Achromobacter sp. DF22	Drilling fluid		
Pseudomonas citronellolis	–	13% for PVC, 30 days	Giacomucci et al. (2019)
Alcanivorax borkumensis	Mediterranean Sea	3.5% for LDPE, 80 days	Delacuvellerie et al. (2019)
Pseudomonas sp	Gulf of Mannar	15% for HDPE, 30 days	Balasubramanian et al. (2010)
Enterobacter asburiae YT1	Indian meal moth (*Plodia interpunctella*) gut	6% for PE, 60 days	Yang et al. (2014)
Bacillus sp YP1		11% for PE, 60 days	
Ideonella sakaiensis 201-F6	PET bottle recycling factory	90% for PET, 50 days	Yoshida et al., (2016)

Jacquin et al., 2019; Jaiswal et al., 2020; Lucas et al., 2008; Moharir & Kumar, 2019; Ru et al., 2020; Sheth et al., 2019; Shimao, 2001; Sivan, 2011; Tokiwa et al., 2009; Wierckx et al., 2015; Zheng et al., 2005). Knowledge has also been summarized for specific plastic types, such as PET (Hiraga et al., 2019; Taniguchi et al., 2019) and PE (Ghatge et al., 2020; Mohanan et al., 2020; Pathak & Navneet, 2017; Restrepo-Florez et al., 2014; Sen & Raut, 2015; Shah et al., 2008), and specific organism groups, such as *Pseudomonas* (Wilkes & Aristilde, 2017).

Ingram's work relied heavily on enzymes encoded by organisms that were bio-prospected from environments rich in the relevant substrate. For example, *K. oxytoca* was isolated from pulp and paper mill waste streams and *Erwinia* is known to be capable of depolymerizing biomass to the point of causing 'soft rot' (Toth et al., 2003). A similar bioprospecting approach has been used to identify microbes encoding enzymes that enable plastic depolymerization and possibly even chassis organisms, with representative findings shown in Table 1. Many of the organisms described to date have been isolated from plastic-dumping sites and landfills, marine water, with utilization of HDPE and/or LDPE being the most frequently described. The gut of wax-eating worms, such as *Galleria melonella*, is also a promising environmental niche from which the PE-hydrolyzing bacteria *Enterobacter asburiae* YT1 and *Bacillus sp.* YP1 were isolated (Bombelli et al., 2017; Cassone et al., 2020; Yang et al., 2014). Bioprospecting has also included the enrichment of naturally occurring microbial consortia capable of plastic degradation, such as marine bacteria with activity on PE (Syranidou et al., 2019) and soil bacteria with activity on LDPE (Esmaeili et al., 2013).

Microbial activity on plastic is affected by polymer type, the condition of the polymer, the identity of the microbial strain and environmental conditions (Artham & Doble, 2008). Such microbial action typically involves enzymes that are secreted onto the polymer surface and/or the production of substrate-specific biosurfactants. As with cellulose, the crystalline nature of plastic waste is a challenge and reductions in the polymer chain length promote further depolymerization (Ghatge et al., 2020). This initial fragmentation of the polymer often occurs due to abiotic environmental factors like UV radiation or mechanical breakdown (Singh & Sharma, 2008), and process designs that include these elements are described below. As with cellulose depolymerization, there is typically a series of enzymatic reactions to reduce the polymer fragments into smaller units, such as dimers and monomers that can then be assimilated into microbial metabolism.

Our understanding of the depolymerization enzymes that are active on the various types of plastic has greatly expanded in the past decade (Chen et al., 2020; Wei & Zimmermann, 2017). Reviews are available describing PET hydrolases (Carr et al., 2020; Maurya et al., 2020) and include achievements in enzyme engineering (Austin et al., 2018). Many of the polymer-degrading enzymes characterized thus far are similar to enzymes known for their ability to depolymerize biologically produced substances (Danso et al., 2019). This raises the possibility that existing design principles and knowledge can be applied to plastic-depolymerizing enzymes.

As with the Ingram group's expression of cellulase enzymes in chassis organisms, the PETase identified from the PET-utilizing organism *Ideonella sakaiensis* was expressed in the photosynthetic algae *Phaeodactylum tricornutum* (Moog et al., 2019). Selection of *P. tricornutum* as the chassis organism was motivated by the intention of its eventual utilization in a marine-type environment. The prospect of using microbial processes not just to degrade plastics but to reassemble the carbon into a valuable molecule was supported by observation of production of the polyhydroxyalkanoate (PHA) biopolymer from LDPE by several bacterial species (Montazer et al., 2019).

Hybrid Processing of Biomass and Plastic Biomass

Economically viable production of low-value fuels and chemicals from lignocellulosic biomass typically uses a hybrid approach involving not just biological activity, but also abiotic mechanical and chemical steps for size reduction and depolymerization (Baruah et al., 2018; Jin et al., 2020; Zoghlami & Paes, 2019). This combination of biological and abiotic steps is referred to here as "hybrid processing."

Methods for pretreatment and depolymerization of lignocellulosic biomass have been reviewed elsewhere (Bhutto et al., 2017; Kumar et al., 2009), including a summary of 20 distinct pretreatment methods across 18 process metrics (Dale & Ong, 2012). The Ingram group frequently used dilute acids for hydrolysis of hemicellulose, though the acid identity changed over time. Their early reports with corn cobs and hulls (Beall et al., 1992), pine wood (Barbosa et al., 1992) and rice hulls (Moniruzzaman et al., 1997) used sulfuric acid. However, other groups demonstrated the advantages of using phosphoric acid instead of sulfuric acid, such as less stringent energy demands and possible means of nutri-

ent economy (de Vasconcelos et al., 2013). The Ingram group described the use of dilute phosphoric acid treatment for biorefining of *Eucalyptus benthamii* and with sugarcane bagasse (Castro et al., 2014; Zeng et al., 2014). In these processes, dilute acid treatment was combined with other abiotic and biological depolymerization steps, such as steam treatment (Castro et al., 2014; Zeng et al., 2014) and the addition of cellulase enzymes (Geddes et al., 2010b).

Processes have been developed that aim to depolymerize of the lignin component for microbial utilization, such as alkaline treatment and pyrolysis (Davis et al., 2019; Davis et al., 2016; Linger et al., 2014; Ragauskas et al., 2014). The heterogenous nature of lignin, and the resulting heterogeneity of any depolymerization products, presents a challenge relative to sugar utilization through central metabolism. The attempt to shunt as much carbon as possible into central metabolic intermediates has been described "biological funneling" (Linger et al., 2014).

Plastics

Abiotic environmental factors, such as weathering and UV radiation, assist in natural biodegradation of plastics (Wilkes & Aristilde, 2017). UV radiation provides energy and promotes free radical formation on the plastic surface, which in turn generates small molecules that can be utilized by microbes (Devi et al., 2016). Similar to the role of acids in hemicellulose hydrolysis, acids can also initiate the oxidation of polymer surfaces (Arkatkar et al., 2010; Kumar Sen & Raut, 2015; Rajandas et al., 2012). It is expected that the design of plastic waste degradation/valorization processes will include some of these components. For example, HDPE was incubated at 70°C for 10 days prior to characterization with microbial substrates, with the goal of enhancing biodegradation (Awasthi et al., 2017).

Pyrolysis has previously been demonstrated as a rapid and robust means of biomass depolymerization. The feasibility of using pyrolysis for plastic depolymerization in combination with microbial valorization was demonstrated with PP (Mihreteab et al., 2019). Specifically, pyrolysis was used to convert PP pellets to an oil rich in fatty alcohols and alkenes. This oil was then utilized by the oleaginous yeast *Yarrowia lipolytica* for the production of lipids. Thermal oxo-degradation of HDPE at moderate temperatures in an oxidative environment was shown to produce a material that supported increased growth of *Candida maltosa* relative to pyrolyzed HDPE (Brown et al., 2022). The fatty alcohols and hydrocarbons produced by pyrolysis or oxo-degradation of plastics will present various challenges relative to the sugars released from lignocellulosic biomass. Such molecules have lower water solubilities and the associated transporters and metabolic pathways are poorly characterized relative to glycolysis (Beier et al., 2014; Hussain et al., 2017; Iwama et al., 2014).

Overcoming Toxicity

Biomass

While there are a variety of effective biomass depolymerization processes, these often result in the release or production of molecules that are inhibitory to the fermentation organism and thus limit the amount of substrate that can be provided, in turn limiting the final product titer (Dale & Ong, 2012; Geddes et al., 2011b). The most well-characterized of these molecules in biomass acid hydrolysate are the small organic acid acetate, released from the biomass, and the aldehyde furfural, a dehydration production of hemicellulose. Other types of biomass treatment methods, such as depolymerization with ionic liquids, also face the issue of organism inhibition (Dickinson et al., 2016). Lignin is often depolymerized into aromatic acids, and these intended substrates are often inhibitory to the production organism (Davis et al., 2019; Davis et al., 2016).

One route for mitigating this toxicity is the addition of a process step to remove or convert the problematic compound(s). The Ingram group demonstrated the effectiveness of the addition of calcium hydroxide "overliming" and removal of the resulting precipitant in improving microbial utilization of acid-hydrolyzed biomass (Martinez et al., 2001; Martinez et al., 2000). This approach has also been shown to be helpful for other types of biomass depolymerization, such as fast pyrolysis (Chi et al., 2013; Liang et al., 2013). The Ingram group also performed a systematic characterization of various detoxification techniques performed individually and in combination (Geddes et al., 2015). It was shown that for sugarcane bagasse phosphoric acid hydrolysate, a combination of vacuum evaporation to remove volatile inhibitors, laccase enzymes, adjustment to high pH with ammonium hydroxide, addition of bisulfite, and finally microaeration was extremely effective, with ethanol production titers lagging only slightly relative to a representative mix of pure sugars (Geddes et al., 2015).

Another route for mitigating this toxicity is to alter the organism so that its sensitivity to the problematic molecules is reduced. This can be done through both evolution-based strain improvement (Jin et al., 2016) and by rational strain engineering (Jarboe et al., 2011). The Ingram group extensively used evolutionary-based strain improvement for tolerance of various products, model inhibitors, industrial operating conditions, and actual biomass hydrolysate (Geddes et al., 2011b; Jarboe et al., 2007; Shanmugam & Ingram, 2021).

Reverse engineering of evolved strains can be used to propose rational strain engineering designs. This was demonstrated by the Ingram group in regards to furfural tolerance (Miller et al., 2009; Turner et al., 2011; Wang et al., 2013) and hydrolysate (Geddes et al., 2011b; Shi et al., 2020; Shi et al., 2016).

Plastics

Given the early stage of characterization of direct microbial utilization of plastics, it is not yet clear if any of the products of biological plastic depolymerization are inhibitory to the associated microbes. One study concluded that there was no negative effect of breakdown products of various plastics on *Penicillium*, *Aspergillus*, and *Pseudomonas* isolates (Taghavi et al., 2021). However, it has been noted that microplastics can increase the tension of lipid membranes (Fleury & Baulin, 2021), and this raises the possibility that membrane engineering strategies may be needed for plastic-utilizing cell factories.

Process Engineering and Scale-Up

Biomass

Bioproduction at rates, yields and titers sufficiently high for economic viability often requires process engineering beyond organism development and substrate depolymerization. For example, the fluid properties associated with operating with a high concentration of depolymerized biomass in the production vessel (high solids) makes it challenging to achieve sufficient mixing (Modenbach & Nokes, 2013). Insufficient mixing can lead to fluctuations in pH, which can negatively impact organism performance (Moniruzzaman et al., 1998). The Ingram group demonstrated that ultrasound could be used to improve microbial utilization of mixed waste office paper (Wood, Aldrich, et al., 1997). The low aqueous solubility of depolymerized lignin can be partially mitigated by preparing emulsions (Davis et al., 2019).

While the depolymerized biomass serves as a source of carbon for the production organism, other macronutrients are needed for

metabolic activity, such as nitrogen (N), sulfur (S), phosphorous (P) and trace metals. The Ingram group observed that crude yeast autolysate could serve as a nutrient supplement (York & Ingram, 1996).

For the production of ethanol from sugarcane bagasse, the Ingram group developed seed train procedures (Geddes et al., 2013), adjusted cellulase usage to improve liquid handling of bagasse slurry (Geddes et al., 2010a), simplified the hydrolysis process (Geddes et al., 2011a) and the saccharification process (Geddes et al., 2010b), identified additional additives to address furfural toxicity (Nieves et al., 2011a) and tuned aeration conditions (Nieves et al., 2011b). This process was operated at the pilot scale (80 L) (Nieves et al., 2011b) and resulting data was used in a technoeconomic analysis of operation at commercial scale (83×10^6 L/yr) in Aspen Plus (Gubicza et al., 2016) and SuperPro Designer (van Rijn et al., 2018). These economic analyses emphasized the need to achieve a high product yield, decrease the cost of cellulolytic enzymes, and add value to lignin.

Plastics

Hopefully, process engineering for microbial utilization of plastics can leverage the expertise that has been developed from lignocellulosic processes. It has been reported that utilization of thermally depolymerized PP by *Y. lipolytica* was increased by the inclusion of biosurfactants (Mihreteab et al., 2019). Many descriptions of microbial utilization of plastic have mentioned biofilms, and these structures were observed to improve LDPE utilization by *Pseudomonas* ASK2 (Tribedi & Dey, 2017). As with biomass utilization, provisioning of nutrients other than carbon will need to be given careful consideration. Characterization of the microbial communities associated with the North Pacific Gyre revealed evidence of nitrogen limitation (Bryant et al., 2016). This observation serves as a reminder that microbes need to be provided with sufficient nutritional support in order to perform the challenging task of plastic utilization and degradation.

Discussion

Here we have attempted to highlight the similarities between the development of processes for the microbial valorization of lignocellulosic biomass and possible processes for the microbial valorization of plastic waste. This review has focused on the work of Lonnie O'Neal (Neal) Ingram and his colleagues at the University of Florida, but the field of lignocellulosic biomass utilization includes many excellent researchers who have made unique and valuable contributions not described here.

This document has mainly described Ingram's work with the production of ethanol from lignocellulosic biomass, but his research group worked with many other biochemical products not described here. Finally, this review has not described Ingram's dedication to commercialization and technology transfer. Neal is often quoted as saying "The development of technology for the cost-effective conversion of modern, renewable biomass into a clean-burning automotive fuel has the potential to free the United States and other nations from oil-dependence and to allow a redistribution of wealth based on productivity and ingenuity rather than natural resources." The assertion of this work is that the development of technology for the cost-effective degradation and valorization of plastic waste has the potential to free the global community from the scourge of plastic waste and that the productivity and ingenuity of our scientists and engineers are sufficient to accomplish this goal for the benefit of all.

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Conflict of Interest

The authors declare no conflicts of interest.

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