Stress-Tolerant Feedstocks for Sustainable Bioenergy Production on Marginal Land

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Abstract Given the mandated increases in fuel production from alternative sources, limited high-quality production land, and predicted climate changes, identification of stress-tolerant biomass crops will be increasingly important. However, existing literature largely focuses on the responses of a small number of crops to a single source of abiotic stress. Here, we provide a much-needed review of several types of stress likely to be encountered by biomass crops on marginal lands and under future climate scenarios: drought, flooding, salinity, cold, and heat. The stress responses of 17 leading biomass crops of all growth habits (e.g., perennial grasses, short-rotation woody crops, and large trees) are summarized, and we identify several that could be considered "all purpose" for multiple stress types. Importantly, we note that some of these crops are or could become invasive in some landscapes. Therefore, growers must take care to avoid dissemination of plants or propagules outside of cultivation.

Keywords Stress tolerance · Bioenergy · Feedstocks · Marginal land · Sustainability

Introduction

Production of second-generation biomass crops is growing in the USA, principally driven by the federal mandate [1] that requires novel feedstocks to offset greenhouse gas emissions from fossil fuels and minimize or avoid any negative impact on the global food supply. Thus, there has been much exploration into biomass crops that are capable of fast growth and high yields on land not suited to food production. Land that is unsuitable for traditional row crops, generally referred to as "marginal" land, may be appropriate for grazing or other uses [2], including biomass crop production. Use of marginal lands for bioenergy production could decrease land-use competition between energy and food crops and ameliorate land-use change associated with biomass crop expansion [3]. However, the fact that this land cannot economically support traditional crop production suggests it is suboptimal in some way and, therefore, may be associated with abiotic stress factors that must be overcome by any crop grown thereon. In addition, the definition of marginal land can also include land with slightly less severe abiotic stressors, potentially supporting some traditional row crops; however, even mild stress may cause those crops to perform suboptimally, causing farmers to operate at a loss, particularly if climate predictions increase the severity of abiotic stress. This paper explores abiotic stressors that may be encountered by biomass crops grown on marginal lands or under changing climate conditions and provides a breadth of options for selecting crops that can tolerate particular types of abiotic stress.

The Asia-Pacific Economic Cooperation (APEC) estimates that marginal lands make up approximately 400 million hectares across Asia, the Pacific Islands, Australia, and North America [4]. Other estimates put the global marginal land area anywhere from 1100 [5] to 6650 million hectares [2], depending on the parameters used to describe marginal (e.g., "non-favored agricultural land," "abandoned or degraded cropland," or arid, forested, grassland, shrubland, or savanna habitats). The potential area available in the USA for cellulosic biomass crops and low-input, high-diversity native perennial mixtures ranges from 43 to 123 million hectares [5, 6]. The differences in these estimates reflect the inconsistencies in the usage of the term "marginal land," despite its common use in

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the bioenergy industry and literature [5, 7, 8]. Marginal lands are often described as degraded lands that are unfit for food production and/or of some ambiguously poor quality and are often termed unproductive [7]. Unproductive soils are characterized by unfavorable chemical and/or physical properties that limit plant growth and yield, including low water and nutrient storage capacity, high salinity, toxic elements, and poor texture [4, 9]. Further difficulties encountered in marginal landscapes include shallow soil depth due to erosion, poor drainage, low fertility, steep terrain, and unfavorable climate [2]. Despite the poor quality of marginal land and the potential problems it could present for its production, biomass is unlikely to be grown on high-quality land that is economically viable for traditional crops [7].

Climate change will exacerbate the issue of land marginalization and degradation [10, 11]. It has been predicted that negative impacts of climate change will increase over the next 25 years, with longer growing seasons (frost-free periods), increasing extreme precipitation events (both flooding and drought), fewer chilling hours, and a greater number of hot nights projected for most growing regions of the country [11]. Because these changes are projected to occur to a greater extent in certain regions of the country [11], crop production—potentially including biomass crops on marginal lands—may shift to novel regions where different stressors are present or growers may shift to different production systems. For example, to escape the predicted hot nights in the southeast, growers may shift to more northern regions where precipitation may be less frequent [11]. These changes will—and already do—directly affect the physiology and reproductive development of many crop plants, including first generation biomass crops [12, 13]. Therefore, it will be important to select the most tolerant crops suitable for future climate scenarios [14].

In this work, we review and summarize the literature on the effects of three sources of abiotic stress that may be common to marginal lands—moisture, salinity, and temperature—and identify biomass crops that display tolerance to these types of stress. Our discussion is geared toward the USA but could be applied to similar circumstances in other regions. Although most plant matter has the potential to be converted into energy, we focus on the promising non-food crops identified in the US Department of Energy's Billion Ton Update [15] and in novel research programs that are investigating the next wave of potential biomass crops. Each of the crops in our report has been the subject of detailed study, investigating ecological, agronomic, physiological, or molecular responses to one or more stressors. Our goal is not to restate the detailed results of these studies, but instead to provide a comprehensive review of the effects of multiple stressors in the context of bioenergy production and a useful guide for growers to choose the best biomass crop for stressful growing conditions.

Moisture Stress

Framing the Issue

Water scarcity is the most limiting environmental factor to crop growth and yield [16] and is a major factor in the categorization of lands as "marginal" or unsuitable for crop production [17]. Drought is a prolonged period of time without significant precipitation, resulting in a shortage of water [18]. More frequent, severe, and longer-than-average duration of drought is predicted in the USA and globally due to changing climate conditions [11, 14, 19–21]. In addition to large-scale climatic factors, effects of drought can be exacerbated by local or regional factors including aridity, topography, or soil conditions [22]. Marginal lands are often characterized by sloped topography or eroded soils with little moisture-holding capacity [23]; therefore, the effects of drought-inducing climate changes have the potential to be stronger in these landscapes [10, 11]. For example, Lee et al. [24] observed that drought effects on biomass yield of perennial grasses varied according to topography, with greater effects at higher elevations.

Conversely, soils with poor drainage—and with the potential for flooding or waterlogging—are also typical of numerous marginal landscapes [23]. Many native Midwestern soils were poorly drained and unsuitable for annual crop production before an extensive network of tile drains were installed [23]. However, marginal land not in crop production is unlikely to have been tiled and therefore may be subject to problems associated with waterlogging in wet years or on wet sites. However, poor drainage is not only an issue in the Midwest. More than half of the freshwater wetlands in the USA have been drained or filled for agricultural use [25], and some have been or will be abandoned due to insufficient drainage [26]. Because rainfall events have become heavier and more frequent in recent years—and this trend is predicted to continue [11]—poorly drained soils can quickly become flooded or waterlogged.

Effects of Moisture Stress

Tissue expansion, dependent on cellular turgor pressure, is strongly tied to water availability, and plant growth is therefore limited by water deficits. This impacts germination, seedling growth, and stand establishment, and leads to reduced plant height, leaf area (both in size and number), and crop yield [27]. In adult plants, drought effects on shoot tissue expansion are generally more severe than in roots, which are less sensitive to water deficit stress [28]. Cellular dehydration inhibits photosynthesis under severe drought stress, resulting in reduced levels of carbon assimilation [29, 30]. Continued respiration under dry conditions can lead to a negative carbon balance in drought-affected plants [27]. This is due to the

combined effects of decreased carbon assimilation overall and decreased translocation of photosynthates from leaves through phloem, which requires maintenance of cellular turgor [29]. Transpiration is inhibited in most plants under water deficit stress, due to stomatal closure and xylem cavitation, and this can lead to decreased nutrient uptake [27]. Prolonged periods of stomatal closure can also lead to heat stress (see Moisture Stress Tolerance Strategies below), as plants cannot employ transpirational cooling to reduce heat load. Reproductive structures, including both flowers and fruits, can also be severely affected by water deficit stress, due to reductions in the availability of photosynthates, inability to achieve turgor required for cellular expansion and tissue growth, and disruption in the activity of key enzymes [27]. Additional effects of water deficit have been described, but the above represent the most common impacts on plant growth and functioning.

Flooding primarily affects plants by reducing soil oxygen availability and therefore reducing root respiration [31]. Water replaces oxygen in soil pores, causing hypoxic or anoxic conditions that not only limit the diffusion of oxygen but also promotes the growth of anaerobic bacteria, which produce toxic compounds that could harm plants [29]. Many sensitive plants respond to waterlogged conditions by closing stomata, which reduces whole-plant water potential gradients and xylem transport [31, 32]. Further, waterlogged roots are unable to absorb nutrient ions, leading to nutrient deficiency symptoms in shoot tissue [29]. Similarly, the rate of photosynthate transport from leaves to roots can decrease by more than half within 30 min of flooding; this photosynthetic inhibition is not well understood, but it is thought to be linked to the toxic products of anaerobic respiration [32]. Plants sensitive to flooding are severely damaged within hours, with decreased growth, survival, and yield [29]. Plants with moderate flood tolerance are able to withstand anoxic conditions temporarily, although some can be damaged after multiple days of waterlogging. Strategies of highly flood-tolerant taxa will be discussed further below.

Moisture Stress Tolerance Strategies

True drought tolerance is the ability to grow, flower, and produce favorable yields under suboptimal water supply [27]. There are three major types of drought tolerance: drought escape, desiccation postponement or avoidance, and desiccation tolerance [29]. The life cycles of drought escapers are completed during wet seasons or while well watered [27, 29], and therefore, these plants do not necessarily possess physiological adaptations to drought stress. Desiccation postponers/avoiders maintain tissue hydration under drought conditions, while plants tolerant of desiccation perform metabolic functions even while dehydrated [29]. Several morphological, molecular, and physiological mechanisms, including

alteration of root/shoot ratios, osmotic adjustment, and production of dehydrin proteins, are important in drought tolerance and are covered elsewhere in comprehensive reviews [e.g., 33–37]. While we will not detail these mechanisms here, it is important to note that plants employing the three different photosynthetic pathways (C3, C4, and crassulacean acid metabolism (CAM)) show inherent drought tolerance and water use efficiency differences.

Stomatal closure helps to reduce the ratio of transpiration-to-water uptake and delay dehydration [28]. Species with C4 and CAM photosynthetic pathways benefit from fixing a high rate of CO_2 with partially or fully closed stomata [38–40] and are generally considered more drought tolerant than most C3 species. Plants employing C4 photosynthesis also have higher water use efficiency (WUE), as well as increased biomass production in both ideal and drought conditions [41, 42]. The extensive root systems of perennial C4 grasses also maximize water uptake from the soil [43]. CAM plants take up CO_2 at night, making them better suited for chronically dry environments than C3 and C4 plants [44]. It has been estimated that CAM crops require only 20 % of the irrigation of the most efficient C3 and C4 crops [44].

Mechanisms for flood tolerance, including hormonal, molecular, and physiological mechanisms, have been reviewed in detail by a number of authors [e.g., 45–47]. Major morphological adaptations to flooding include production of aerenchyma tissue, enlargement of stem lenticels, and development of new roots [31]. Movement of oxygen to roots through aerenchyma not only allows root cells to reestablish aerobic respiration but also decreases toxic compounds outside of the root cortex through diffusion into soil and oxidation of reduced soil ions [32]. Formation of adventitous roots can compensate for decreased absorptive capacity or death and decay of existing roots and can lead to reopening of closed stomata [32].

Drought- and Flood-Tolerant Biomass Crops

As discussed previously, we searched for stress tolerance literature relating to several promising biomass crops being cultivated or developed in the USA currently. It is important to note that, as a consequence, our list of tolerant biomass crops should not be considered exhaustive. In addition, many of the available studies were designed to test relative tolerance among varieties or species. Thus, this analysis is not meant to provide absolutes or guarantee stress tolerance under every circumstance. However, our analysis still represents a more comprehensive review of multiple biomass crops and multiple stressors than currently exists. Table 1 details evidence of drought stress tolerance, and Table 2 details evidence of flooding tolerance in 17 biomass crops.

Of the 17 crops evaluated, six species were highly drought tolerant, and others had drought-tolerant species or genotypes

Table 1 Drought tolerance in 17 feedstocks with bioenergy potential

Taxa	Ps type	Tolerance level	Evidence of drought tolerance
Agave spp.	CAM	High	Evolved in arid habitats [48] sunken stomata [48], elastic cells, shallow roots, osmotic adjustment, root isolation from dry soils [44]; CAM crops require 20 % of the irrigation of the most efficient C3 and C4 crops [44].
Andropogon gerardii	C4	High	Greater allocation to roots, reduced allocation to flowering, more rapid leaf turnover, and more rapid recovery of photosynthesis after wilting, relative to *Sorghastrum nutans* [49]. Able to maintain carbon gain at lower water potentials than *Panicum virgatum* [50].
Arundo donax	C3	Low	Not tolerant, but can survive drought [51, 52].
Eucalyptus spp.	C3	High	Some taxa (e.g., *Eucalyptus rameliana* and *Eucalyptus pachyphylla*) occupy arid habitats with <350-mm annual precipitation [53]; Drought-tolerant genotypes of *Eucalyptus globulus* display multiple drought tolerance strategies, including more developed root system, smaller seeds with desiccation tolerance, greater ABA content, and accumulation of proteins involved in stress tolerance [54].
Helianthus annuus	C3	Nil	Not tolerant [55, 56], but certain cultivars and relatives could be used in breeding programs to increase tolerance (e.g., *Helianthus argophyllus* [57] and dwarf *Helianthus annuus* cultivars [55]).
Jatropha curcas	C3	High	Drought avoidance through selective leaf abscission, decreases in Ps and WUE, maintaining above lethal water potential and ability to recover quickly [58].
Miscanthus spp.	C4	Moderate	*Miscanthus × giganteus* leaf area and yield reduced under drought stress [59], but water availability does not affect shoot production or plant height at the beginning of the growing season [60]. *Miscanthus sinensis* has good drought tolerance [61] and could be included in future breeding programs to improve tolerance in *Miscanthus* hybrids [62].
Panicum virgatum	C4	Moderate to high	Germination and biomass yield reduced under extreme drought [63], but after establishment, all plants survived at −4 MPa [64]. Generally very tolerant of moderate or even extreme drought [65] especially if adequate rainfall occurs early in the growing season [66]. Upland cytotypes are more drought tolerant than lowland types [67, 68].
Pennisetum purpureum	C4	High	Requires good moisture during establishment, but acquires tolerance in later stages [69]; repeated drought stress did not affect biomass yields, but plant height was reduced after multiple drought treatments [70]. Several highly drought-tolerant genotypes could be used to further improve tolerance [71]
Pinus spp.	C3	Varies	Drought-tolerant species: *Pinus bungeana* [72], *Pinus cembra* [72], *Pinus echinata* [72, 73], *Pinus elliottii* [72, 73] *Pinus flexilis* [72], *Pinus glabra* [73], *Pinus heldreichii* [72] *Pinus korariensis* [72], *Pinus mugo* [73], *Pinus nigra* [72], *Pinus palustris* [73], *Pinus rigida* [72], *Pinus sylvestris* [76, 77, *Pinus taeda* [72, 73] *Pinus thunbergiana* [72], *Pinus virginiana* [73], *Pinus wallichiana* [72].
Populus spp.	C3	Varies	*Populus euphratica* experiences drought-induced xylem cavitation [74], but calcium-dependent protein kinase confers drought tolerance [75]; transgenic *Populus deltoides* ("NL895") is drought tolerant [76]. Drought tolerance in *Populus nigra* varies among clones [77].
Robinia pseudoacacia	C3	High	Listed as a drought-tolerant species in extension publications [76 77; tetraploid clones achieved greater biomass, WUE, and photosynthesis rate than common diploid clone [78]
Saccharum spp.	C4	Varies	*Saccharum spontanaeum* cane yield, leaf area, plant height, and photosynthesis rate were reduced under drought [79], but genotypes Co 99004 and Co 99012 [79] and BOT-53, BOT-54, and BOT-6 [80] were more tolerant and productive; *Saccharum officinarum* root/shoot ratio, WUE, and rate of height growth were not affected by drought, but biomass, root factors, and stalk diameter were reduced. Genotypes 03-4-425 and Phill66-07 were more tolerant [81]. Transgenic sugarcane with introduction of AVP1 *Arabidopsis* gene was more tolerant [82].
Salix spp.	C3	Varies	*Salix cinerea* [83], *Salix elaeagnos* [84], *Salix gooddingii* [85], and *Salix matsudana* "Navajo" [86] are more drought tolerant than other species.
Sorghastrum nutans	C4	Varies	*Sorghastrum nutans* var. "Tejas" is better adapted for germination and early growth in dry conditions than "Cheyenne" or "Lometa" [87].
Sorghum bicolor	C4	High	No negative effect on ethanol yield (actually increased EtOH yield if drought imposed during early flowering), especially in hybrid DK-28E [88], drought tolerant through avoidance has deep and extensive root system—and true tolerance—osmotic adjustment allows stomata to stay open and metabolism to continue [89].
Spartina pectinata	C4	Low	Not tolerant due to thin leaves, thin cuticle, and adaptation to wet conditions [90].

within the genus (Table 1). Several of the most tolerant taxa were C4 perennial grasses, including *Andropogon gerardii*, *Pennisetum purpurem*, and *Sorghum bicolor*. For example,

Sorghum bicolor is highly productive in dry African climates [109], likely due to the high WUE and large root systems found in many cultivars [110]. *Panicum virgatum* shows low

Table 2 Flooding tolerance in 17 feedstocks with bioenergy potential

Taxa	Ps type	Tolerance level	Evidence of flooding tolerance
Agave spp.	CAM		N/A
Andropogon gerardii	C4		N/A
Arundo donax	C3	Moderate	Biomass decreased (~50 %) in flooded vs well-watered soil [51]; biomass and rhizome viability unaffected by flooding [52].
Eucalyptus spp.	C3	Varies	*Eucalyptus camaldulensis* is flood tolerant [53, 91, 92]; *Eucalyptus camaldulensis* > *Eucalyptus globulus* > *Eucalyptus obliqua* in level of flood tolerance [91], though even *Eucalyptus camaldulensis* showed some reductions in growth, biomass, and photoassimilate transport [92]; *Eucalyptus camaldulensis* requires seasonal flooding for regeneration [53].
Helianthus annuus	C3		N/A
Jatropha curcas	C3	Low	Flooding sensitive [93].
Miscanthus spp.	C4	Moderate	*Miscanthus* × *giganteus* biomass and rhizome viability unaffected by flooding [52].
Panicum virgatum	C4	Moderate	Seedlings emerged and established at all moisture conditions (−0.3 MPa to flooded). Transplants of lowland ecotypes performed as well in flooded conditions as in field capacity controls. Flooding reduced performance of upland ecotypes [64].
Pennisetum purpureum	C4	Moderate	Compared with corn and mungbean (*Vigna radiata*), *Pennisetum purpureum* maintained higher stomatal and mesophyll conductance, allowing for continued CO_2 assimilation under flood stress [94].
Pinus spp.	C3	Varies	Almost 100 % of *Pinus elliotti* survived up to 40 days of flooding up to 60 cm [95]; *Pinus echinata*, *Pinus taeda*, and *Pinus rigida* var. *serotina* were all resistant to flooding. Standing water for 12 weeks produced slightly less growth relative to running water treatment and field capacity treatment [96]. Once established, *Pinus sylvestris* can withstand waterlogging for a long period (25 months in this study) [97].
Populus spp.	C3	Varies	*Populus deltoides* × *Populus nigra* hybrid cv. "I-488" was more flood tolerant than other hybrids, especially with some pre-exposure to flooding [98]; *Populus deltoides* hybrid "Alton" was flood tolerant (least loss of leaf area and production of adventitious roots compared to other hybrids [99]. *Populus deltoides* "Alton" tolerates floods because stomatal conductance and root membrane integrity remain functional [100].
Robinia pseudoacacia	C3	Low	Intolerant—did not survive continuous flooding during one growing season [101].
Saccharum spp.	C4	Varies	Japanese sugarcane (*Saccharum* spp. var. "NiF 8") roots, leaves, stalks, sugar content (brix), and dry weight increased in response to flooding [102]; juice quality decreased from waterlogging and mean fiber content increased in waterlogged conditions. There were differences among sugarcane varieties, but sugar yield was reduced in waterlogged conditions across varieties [103].
Salix spp.	C3	Varies	*Salix petiolaris* was least susceptible to flood-induced dieback, and *Salix planifolia* and *Salix exigua* were intermediately susceptible (*Salix bebbiana* and *Salix discolor* were most susceptible) [104]. In general, willow cover decreased on wetter transects over time (1993–2001), and increased on drier transects [104]. *Salix elaeagnos* established and survived in flooded conditions [84].
Sorghastrum nutans	C4	Low	Compared with other native warm-season grasses tested and although pot studies suggested moderate flood tolerance, *Sorghastrum nutans* performance in flooded riparian sites was poor [109].
Sorghum bicolor	C4	Moderate	Thirty days after seed germination, sorghum generally tolerates waterlogging (no effect on shoot growth). Some varieties form aerenchyma and adventitious roots [89].
Spartina pectinata	C4	High	*Spartina pectinata* is flood tolerant, with little change in photosynthetic capacity in flooded conditions [105]. *Spartina pectinata* is the dominant species in low prairie where soils are too wet for switchgrass, maize and other grain, forage, and biofuel crops. Can also produce high biomass on well-drained soil on prime land and on coarse-textured soil on dry marginal land [106]. *Spartina pectinata* grew best under prolonged inundation (4 weeks), compared with alternating dry and wet conditions [107], and performed better than other warm-season grasses in riparian conditions [108].

N/A no supporting evidence was found in literature databases

tolerance during establishment [64], possibly because of lower water use efficiency related to lower carbon assimilation during drought [111]. Although when drought was imposed after establishment, *Panicum virgatum* plants appeared to be drought hardy [64, 65]—particularly upland cytotypes [67, 68]. In addition, a long-term field evaluation of biomass crops (34 herbaceous taxa assessed over 10 years across a wide range of soil and sites) indicated that *Panicum virgatum* and certain *Sorghum bicolor* varieties outperformed other crops under drought conditions [112]. As expected, the one CAM crop we included in our database, *Agave* spp., showed high drought tolerance due to several morphological and

physiological adaptations to the arid climates in which it evolved [44, 48]. A number of woody crops were also drought tolerant, depending on genotype. These included several *Eucalyptus* species, *Jatropha curcas*, several *Pinus* species, *Populus* hybrids, *Robinia pseudoacacia*, and several *Salix* species (Table 1). Several studies identified particular genotypes that were more drought tolerant than the wild type (e.g., sugarcane genotype Co 99004) or identified congeners with higher tolerance than the target crop (e.g., *Helianthus argophyllus*) (Table 1). This information could potentially be used in future breeding programs to develop more tolerant biomass crops for marginal lands.

Several species and genotypes have evolved in wetland conditions and are moderately to strongly tolerant of flooded conditions (Table 2). For example, because *Spartina pectinata* is native to North American moist prairies, marshes, and drainage ways [113], it can be grown in soils that are too wet to grow corn, big bluestem, or switchgrass [114, 115], although lowland types of switchgrass are tolerant of flooded conditions [64, 68]. Other flood-tolerant crops include *Eucalyptus camaldulensis*, *Miscanthus × giganteus*, several hybrid *Populus* spp., *Pinus elliotti*, and *Sorghum bicolor* (Table 2). *Eucalyptus camaldulensis* formed adventitous roots and maintained moderate growth rates in flooded conditions [32], while the most tolerant *Populus* hybrids allocated more carbon to belowground structures, formed adventitious roots, and maintained stomatal function, net photosynthetic rate, and relative growth rate [116]. Again, novel genotypes of traditional crops showed greater flood tolerance than their parents, highlighting the potential for improvement in these and other taxa (Table 2). One example is a Japanese sugarcane (*Saccharum* spp.) hybrid which showed an increase in dry biomass in response to flooding. Continuous flooding is often deleterious to sugarcane growth [117], but because it is typically cultivated in wet tropical regions, it is important to develop varieties that are productive under flooded conditions.

Several of the focal biomass crops have not been the subject of study related to flooding tolerance (i.e., "N/A" in Table 2), but this lack of evidence should not be interpreted as flood sensitivity for these taxa.

Salt Stress

Framing the Issue

Salinity is a major environmental stressor affecting arid, semi-arid, and irrigated land worldwide [118, 119] and contributing to the abandonment or marginalization of land [118]. Salinization can occur naturally, through aerosolization, deposition, or contact with sea salts in coastal locations [120], or through proximity to saline seeps, shallow water tables, and

degradation of parent rock materials inland [121, 122]. Alternatively, so-called "secondary salinization" occurs anthropogenically, as a result of replacing deep-rooted native vegetation with shallow-rooted crops and pasture or from adding irrigation water to soils [120, 123]. Both actions can result in changes to water table depth, causing salts to accumulate in the root zone as excess water evaporates from the soil surface [120, 123]. While some dissolved salts can improve soil texture, an excess of salts, including sodium, can cause soil dispersion and reduced permeability [124]. Salt accumulation can render soil unsuitable for many traditional food crops by decreasing plant-available water and creating toxic cellular products [29].

More than 6 % of the global land area (>800 million hectares) [125] and at least 8.5 million hectare in the USA [124] are salt-affected. Secondary salinity, resulting from irrigation or land clearing, affects 20 [125] to 50 % [118, 126] of the irrigated land area globally. There is evidence that the land area affected by salinization is growing through anthropogenic causes [127] and due to changing hydrologic patterns related to climate change [128], resulting in an increasing proportion of marginal land. However, production of tolerant biomass crops on salt-affected soil could result in soil quality improvement and soil carbon sequestration [129].

Effects of Salt Stress

Effects of salinity on plant growth and physiology have been reviewed comprehensively elsewhere e. g [130–132], but common effects are discussed here. Under prolonged or severe salt stress, plants can experience negative developmental effects [126], from seed germination [133] and emergence [134] through maturation [135]. Dissolved salt ions in the soil solution can substantially reduce osmotic potential values (typical saline soil water potentials range between −1.6 and −10 MPa [136]), altering water potential gradients that drive water uptake and solute movement through plant tissues [133], resulting in decreased water uptake even when soils are wet. This functional reduction in water availability can lead to symptoms typical of drought-affected plants: reduced shoot and root growth rates, reduced leaf number, declines in stomatal conductance and photosynthesis rates, and damage or death of leaves [30, 130, 137–139]. In addition, salt ions can cause cellular toxicity, as well as disruption of normal membrane functioning, nutrient uptake, protein synthesis, and enzyme activation [29]. Secondary effects, including oxidative damage [140] and cell death, can also result from salt stress.

Salt Stress Tolerance Strategies

Halophytes ("salt-loving" plants) have specialized strategies for growth in saline conditions [130, 141–143]. These include succulence, which maintains water-to-salt ratios at acceptable levels as the overall cell volume increases,

compartmentalization of salt ions into vacuoles or specialized salt glands on leaf surfaces, and efficient ion pumping mechanisms to exclude or remove ions from cytosol into plant apoplast [29]. However, halophytes are not the only plants that can tolerate salinity. Because saline soils are functionally similar to dry soils, plants with high water use efficiency (e.g., C4 and CAM plants) are predicted to perform well when exposed to salinity. In addition, many plants are capable of moderate levels of osmotic adjustment, in which salts accumulate in vacuoles to maintain cellular turgor and reestablish whole-plant water potential gradients. This adjustment takes place over a matter of hours to days [130], during which time growth is restricted and wilting may occur. More salt-tolerant plants go beyond compartmentalizing salts into vacuoles by excluding NaCl from xylem channels, actively exporting Na^+ into the soil solution, and regulating K^+ loss in cation channels [80]. Several comprehensive reviews offer additional information about salt tolerance mechanisms [e.g., [125, 144, 145].

Salt-Tolerant Biomass Crops

Some potential biomass crops, such as *Pennisetum purpureum*, show no more salinity tolerance than conventional agricultural crops [146, 147]. Thus, the current challenge is to find biomass crop species that can grow and maintain high yields on marginal salt-affected soils. Of the 17 crops evaluated, several species or genotypes were highly tolerant of salinity (Table 3). Deep-rooted perennial grasses are often recommended for drought- and salt-affected soils [180–183], and our literature search corroborated this recommendation. However, some of these grasses were more tolerant than others. For example, *Andropogon gerardii*, *Arundo donax*, and *Spartina pectinata* were highly salt tolerant, with the latter two classified as halophytes [152, 179]. In contrast, *Pennisetum purpureum* showed major reductions in shoot biomass in saline conditions [146], and *M. × giganteus* was only moderately salt tolerant [160]. Upland ecotypes of *Panicum virgatum* (e.g., "Blackwell," "Trailblazer," and "PV-1777") were among the more salt-tolerant cultivars [151, 164, 166, 184], although the upland ecotype, "Cave-in-Rock," was not tolerant at the seedling stage [167].

Several salt-tolerant woody crops are also available (Table 3). For example, *Eucalyptus camaldulensis* cultivars "Silverton" and "Local" efficiently excluded or compartmentalized salts in saline and saline + hypoxic conditions [154]. *Pinus pinea* showed no growth reduction under saline conditions [168], and *Pinus banksiana* growth may have been stimulated by certain levels of salinity [169]. Among tree crops, short-rotation woody crop (SRWC) species have particularly strong bioenergy potential because of fast growth and high yields [185–188]. Salt-tolerant SRWC species include several poplar (*Populus* spp.) and willow (*Salix* spp.) hybrids and tetraploid *Robinia pseudoacacia* (Table 3). These hybrids

and others identified in Table 3 highlight the possibility of breeding salinity tolerance into many of the biomass crops destined for production on marginal lands.

Temperature Stress

Framing the Issue

Temperature is a major factor governing plant growth and biomass production [189], and temperature extremes can cause severe abiotic stress and inhibit plant growth. Climate comparisons between the most recent decade and historical climates indicate unmistakable and consistently warming surface temperatures on a global scale and throughout much of the USA; however, some small regions in the southern USA are now experiencing cooler than average trends [190]. Irrigation and soil amendments in traditional production systems may offset some of the negative effects of heat and cold temperatures [191]. In order to avoid heat-related crop damage, some growers may also opt to shift production to alternate regions where summer temperatures are milder. However, moving perennial crops to more northern locations will introduce more extreme winter weather to crops that may be adapted to mild winter climates. In addition, thermal climate changes may impact crops grown on marginal lands to a greater extent than prime agricultural land [192]. With greater temperature fluctuations and movement of crops outside of their traditional production regions, it will be important to develop biomass crops that can tolerate temperature extremes.

Effects of Temperature Stress

All plant species are adapted to a range of optimal temperatures, but when they are subjected to temperatures outside that range, physiological, metabolic, and molecular changes occur to maintain homeostasis under suboptimal conditions [193]. If the plant experiences suboptimal temperatures for an extended period, these processes become more impaired and abnormal until temperatures reach lethal levels [193]. Both low and high temperatures can cause physiological stress symptoms and physical damage in plants. Low-temperature stress can be caused by both freezing (temperatures less than −1 °C) and chilling (0–18 °C). The injuries caused by low temperatures for both freezing and chilling can be seen within 48 to 72 h and may include phenotypic changes (e.g., wilting, reduced leaf expansion, chlorosis, and necrosis) [193]. Reproductive processes and structures are also severely affected by cold, which can lead to pollen and flower sterility [193]. Likewise, exposure to cold in the germination and establishment phases can lead to low germination rate, stunting of seedling growth, chlorosis, and reduced tillering in grasses [193]. On a physiological level,

Table 3 Salinity tolerance in 17 feedstocks with bioenergy potential

Taxa	Ps type	Tolerance level	Evidence of salinity tolerance
Agave spp.	CAM	Low, but variable	*Agave parryi* var. *truncata* fresh weight, dry weight, and moisture content decreased as salinity levels increased [148]. *Agave sisalana* shoot and root growth was reduced at higher salinity levels. Height was also reduced but not as much as in some other species. Characterized as intermediately tolerant [149]. *Agave deserti* seedlings very sensitive to salinity [150].
Andropogon gerardii	C4	High	*Andropogon gerardii* had the highest germination rates under increased salinity levels, compared with other C4 grasses [151].
Arundo donax	C3	High	High resilience to high-salinity tannery effluent wastewater [152]; high biomass production when grown in former salt evaporation pond, and when irrigated with water 90 % the salinity of seawater [153]. Described *Arundo donax* as a halophyte [153].
Eucalyptus spp.	C3	Varies	Twenty species can grow in saline conditions (e.g., *Eucalyptus robusta* and *Eucalyptus camaldulensis*) [53]. *Eucalyptus camaldulensis* "Silverton" and "Local" did better in salinity and saline + hypoxic treatments than *Eucalyptus tereticornis*, which was sensitive to salinity and hypoxia. *Eucalyptus camaldulensis* "Silverton" and "Local" use different strategies, with "Silverton" using tissue compartmentalization and "Local" using tissue exclusion [154].
Helianthus annuus	C3	Varies	Several genotypes, particularly cytoplasmic male sterile (CMS) lines, performed well in high-salinity conditions [155]; some genotypes show evidence of salinity avoidance by excluding salts at the root level, while resistant lines change biomass partitioning patterns [156].
Jatropha curcas	C3	Moderate	Characterized as moderately tolerant [157] at salinity levels up to 100 mM NaCl [158]; salinity alone was tolerated by *Jatopha curcas*, but salinity (100 mM NaCl) + heat was harmful to CO_2 assimilation and membrane functioning [159].
Miscanthus spp.	C4	Moderate	Salinity above 100 mM affected *Miscanthus × giganteus* growth, with rhizomes > roots > shoots in order of increasing sensitivity (rhizomes least sensitive). Plants grown from larger rhizomes initially were less sensitive [160]. Some accessions of *Miscanthus sacchariflorus* were highly salt tolerant during germination and could be used to improve future hybrids [161]. Salt tolerance during germination was better in *Miscanthus floridulus* collected from lowland locations in Taiwan, suggesting the possibility that salt-tolerant germplasm exists and could be used for future hybrids [162].
Panicum virgatum	C4	Moderate	Salinity had no effect on germination and survival under low-alkaline pH, but when salinity was combined with higher pH, germination and survival were strongly reduced [163]. *Panicum virgatum* is moderately tolerant of saline conditions, and cultivar "PV-1777" had the highest salinity tolerance for upland ecotypes in one study [151], but in others, "Blackwell" [164, 165] and "Trailblazer" [166] performed well in high-salinity conditions. Compared with *Spartina pectinata*, *Panicum virgatum* "Cave-in-Rock" had low germination (down 80 %) in high (300 mM) salinity levels, and less than 70 % of seedlings survived in even moderate salinity (100 mM) treatments [167].
Pennisetum purpureum	C4	Low	Salinity inhibits hybrid pennisetum (*Pennisetum americanum × Pennisetum purpureum*) growth, photosynthesis, soluble sugar content, and more, but adverse effects were reduced by applications of nitrate up to 5 mmol/L [147]. The same hybrid can exclude salt from new leaves, but salinity levels of 100 mM results in shoot fresh and dry weight reductions of 50 % compared to controls [146].
Pinus spp.	C3	Varies	*Pinus pinea* showed no significant reduction in growth when grown in 100 mM NaCL hydroponic solution [168]. Of two *Picea* and one *Pinus* species tested, the pine (*Pinus banksiana*) was least affected by salinity during emergence and may have even been stimulated by certain levels of salinity [169].
Populus spp.	C3	Varies (some high)	*Populus × xiaozhannica* cv. "Balizhuangyang" has high tolerance [170]. With respect to salt tolerance, *Populus euphratica* is "outstanding," handling up to 450 mM NaCl [171]. Growth was unaffected in *Populus euphratica* at low-moderate salinity (68 mM), and at 137 mM NaCl, 50 % of *Populus deltoids × Populus alba* "M31" and 100 % of *Populus alba* "GuadalquivirF-21-40," *Populus alba* "GuadalquivirF-21-39," *Populus alba* "GuadalquivirF-21-38," and *Populus euphratica* (100 %) survived [172]
Robinia pseudoacacia	C3	High (in 4n)	Tetraploid black locust can withstand high levels of NaCl and Na_2SO_4 to a greater extent than diploid black locust (e.g., salt injury not observed, no change in water or chlorophyll content, or photosynthesis rate and intercellular CO_2 concentration in 4n). Potentially adaptive changes in leaf anatomy were seen in tetraploid type in response to salinity [173], with the tetraploid version being much more adaptable to salt stress than the diploid [174].
Saccharum spp.	C4	Varies	Transgenic salt- and drought-tolerant sugarcane, with longer and more profuse roots and the ability to withstand higher NaCl, were developed by introducing the AVP1 gene from *Arabidopsis* [82], and sugarcane variety "CP-4333" had the greatest salt tolerance limit at 15.51 dS/m. Characteristics such as pink and waxy-coated stems, large number and area of green leaves, greater root and shoot yield, high-tillering, and ratooning potential revealed positive correlation with salt tolerance and could be used as markers in future breeding programs [175].

Table 3 (continued)

Taxa	Ps type	Tolerance level	Evidence of salinity tolerance
Salix spp.	C3	Moderate	Most willow varieties tested in this study were able to tolerate moderately saline conditions (EC(e)≤5 dS/m). In addition, several varieties ("Alpha," "India," "Owasco," "Tully Champion," and "01X-268-015") showed no reduction in growth with severe salinity (EC(e)≤8.0 dS/m) [176].
Sorghastrum nutans	C4	Varies	*Sorghastrum nutans* var. "Tejas" seeds appeared adapted for optimum germination at higher salt concentrations than "Lometa" or "Cheyenne," but seedlings of those varieties produced greater root and shoot growth at higher salt concentrations than Tejas [87].
Sorghum bicolor	C4	Varies	One hundred genotypes were screened, and seven were salinity tolerant to 250 mM NaCl: "CSV 15," "ICSB 766," "NTJ 2," "ICSV 95030," "S 35," "ICSB 589," "ICSB 676" [177]. Sweet sorghum "Keller" was the most salt tolerant of three cultivars tested, with little reduction in stem yield and soluble carbohydrates [178].
Spartina pectinata	C4	High	*Spartina pectinata* seeds germinated and seedlings survived in high salinity conditions (up to 500 mM NaCl). Under all salinity treatments, cordgrass produced more tillers and greater biomass than switchgrass, by exuding salt through salt glands [167]. *Spartina pectinata* has a level of tolerance to soil salinity that is higher than that of other tall warm-season grasses [106], and that is similar to halophytes [179], with an ability to maintain growth in salinity levels ranging from 2–20 dS/m [180].

this damage can be caused by disruption of membrane and organelle functioning as fluid phosolipids become crystalline and dysfunctional in colder temperatures [193]. In addition, ice crystals can form in apoplastic space, physically damaging cells and causing dehydration through the movement of water out of cells down water potential gradients to join the extracellular ice [193, 194]. Cold exposure can also affect photosynthetic functioning, enzymatic activity [195], protein mechanics, and other metabolic processes [193].

High temperatures can affect plants directly through growth inhibition and indirectly through evaporative water loss [196]. Sensitive species can be affected when air temperatures exceed 35 °C, but tolerant species can withstand air temperatures approaching 65 °C [29, 196]. Most plant species, however, cannot survive for extended periods above 45 °C [29]. As in chilling and freezing stress, membrane stability can be affected by heat. In the case of heat, however, membranes can become excessively fluid, causing ion leakage and inhibition of photosynthesis, respiration, and other processes that involve membrane-embedded proteins and electron carriers [29, 30]. High temperature damage to heat-sensitive photosynthetic components (e.g., chlorophyll, thylakoid membranes, and photosystem II) can significantly affect photosynthetic function [30]. Moderate heat stress can inhibit photosynthesis and thus decrease productivity and yields [197, 198]. Photosynthesis is affected before respiration for most plants, meaning that the production of sugars stops before the demand for them does. This can result in the breakdown of stored sugars (e.g., in fruits, leading to decreased sweetness) [29]. Further, heat stress can significantly reduce ethanol yield of some fuel crops [88]. Additional problems associated with, and responses to, thermal stress are reviewed in greater depth elsewhere [e.g., 196, 197, 199–203].

Temperature Stress Tolerance Strategies

Both cold and heat tolerance can be induced in most species through gradual exposure to non-lethal temperatures. Chilling-resistant species overcome membrane fluidity problems by increasing the proportion of unsaturated relative to saturated fatty acids in the membrane [29, 204, 205], lowering the temperature at which membranes solidify. In addition, sucrose and other soluble sugars accumulate in cells and cell walls to lower the temperature at which freezing can occur and to restrict the growth of ice [29]. Some species, particularly woody taxa, are able to avoid cellular freezing until temperatures dip to −40 °C through the mechanism known as "deep supercooling" [206, 207]. This occurs because of an absence of ice nucleation sites within cells, though ice may form in extracellular spaces. Freezing-resistant species produce antifreeze proteins that halt the growth and spread of ice crystals in extracellular spaces [207, 208].

When ample water is available, most plants are able to cool leaves through evaporative/transpirational cooling [197, 209]. However, when stomata close to prevent water loss in dry conditions, heat damage can occur. Plants adapted to hot climates have evolved morphological adaptations to minimize heat load, including pubescent, vertically oriented, or light-colored leaves [197, 209]. In many plants, increases in temperature initiate translation of heat shock proteins (HSPs), which serve to prevent and repair misfolding of other proteins and facilitate proper cellular functioning at high temperatures [200, 210]. At the whole-plant level, synthesis of HSPs increases tolerance of temperatures that could otherwise be lethal [29, 210]. Although HSPs protect cells against damage, the heat shock response increases the rate of maturation in crops and can decrease yields [211]. Further, the heat shock

Table 4 Cold tolerance in 17 feedstocks with bioenergy potential. N/A indicates no supporting evidence was found in literature databases

Taxa	Ps type	Tolerance level	Evidence of cold tolerance
Agave spp.	CAM	Varies	Species native to higher elevations and latitudes where subfreezing temperatures regularly occur during winter include *Agave utahensis*, *Agave parryi*, *Agave havardiana*, *Agave neomexicana*, and *Agave lechuguilla*. These species or subspecies can survive with no discernible damage to −28 °C or lower [213].
Andropogon gerardii	C4	Moderate	The base temp for germination in *Andropogon gerardii* was among the lowest for warm-season grasses tested, depending on cultivar. "Bison" had the lowest base temp of all species tested, at 2.6 °C, but "Niagara" was one of the higher ones at 5.0 °C. Bison showed some chilling sensitivity symptoms (purpling and partial wilting) during cold exposure, but electrolyte damage was lower for Bison than other cultivars [214].
Arundo donax	C3	Moderate	Cold resistance of five grasses evaluated was, in order: *Arundo donax* (−21.3 °C) > *Arundo* sp. (−12.05 °C) > *Echinochloa crusgalli* (−1.98 °C) > *Pennisetum purpureum* (0.69 °C) > *Pennisetum* sp. (0.18 °C). Study evaluated semi-lethal temperatures (LT 50) [215].
Eucalyptus spp.	*C3*	Varies	Some small trees or shrubs (e.g., *Eucalyptus coccifera* or *Eucalyptus pauciflora* ssp. *niphophila*) are adapted to subalpine conditions [53]. *Eucalyptus occidentalis* showed low cold tolerance, with foliage death due to frost occurring at −4 °C [216] A freeze-tolerance gene has been introduced into *Eucalyptus urograndis* elite clone EH1, and resulting trees are tolerant to freezing temps to −8 °C [185].
Helianthus annuus	C3	Low	Carbon assimilate translocation was inhibited in cold (13 °C) grown sunflower, and photosynthesis rate was lower than in warm (30 °C) grown sunflowers [217]. Eighteen germplasm lines were found to be frost resistant, and two (NDCMS-1B and NDLR-2) escaped frost damage by flowering early [218].
Jatropha curcas	C3	Low	Very low tolerance [157], but chilling tolerance can be induced in seedlings if exposed to a 5 °C chilling shock followed by a recovery period at optimal temperatures (26 °C) [219].
Miscanthus spp.	C4	Moderate	The lethal temperature at which 50 % (LT50) of *Miscanthus × giganteus* rhizomes were killed was −3.4 °C, which can be problematic especially during first winter. In *Miscanthus sinensis*, LT50 was −6.5 °C [220]. *Miscanthus × giganteus* shows unusual cold tolerance for a C_4 species [60]. *Miscanthus sinensis* grows where Tmin is down to −11 °C [221].
Panicum virgatum	C4	Moderate	The base temp for germination in *Panicum virgatum* was among the lowest for warm-season grasses tested, depending on cultivar. "Dakota" had one of the lowest base temperatures of all grasses, at 2.79 °C, but the other three switchgrass cultivars ranged from 4.5 to 7.3 °C with Cave-in-Rock (CIR) the highest. No symptoms were seen during chilling treatment, but some after recovery. Leaf damage ranged from 40 to 56 % across cultivars, with CIR having the highest leaf area damage of all warm-season grasses tested. Electrolyte leakage was lowest in "Dakota" compared with all other grasses tested, and CIR was close to the highest [214]. Lowland cytotypes are particularly susceptible to cold winter conditions, as they are adapted to southern latitudes [222, 223]. *Panicum virgatum* shows unusual tolerance to cold night temps for a C_4 grass [224].
Pennisetum purpureum	C4	Low	Growth rate and productivity of *Pennisetum purpureum* was greater than corn at chilling temps, but chilling reduced leaf extension, leaf area, and chlorophyll content in *Pennisetum purpureum*. Roots were more resistant to chilling than shoots [225]. The semi-lethal (LT50) temperature for *Pennisetum* spp. (0.18 °C) was the highest of all grasses tested [215].
Pinus spp.	C3	High	Some pines are frost hardy to −70 °C, including *Pinus sylvestris* [226]. Conifers are among the most cold-tolerant of vascular plants, with twigs of some pine species withstanding temps as low as −196 °C [202].
Populus spp.	C3	High	A calcium-dependent protein kinase gene in *Populus euphratica* confers drought and cold stress tolerance [75]. *Populus deltoides* ssp. *monilifera* survived cooling to −70 °C [227].
Robinia pseudoacacia	C3	High	Withstands cold and freezing temperatures by increasing fatty acid concentration [228] and protein synthesis in bark cells [229, 230], and produces glycoproteins to prevent ice crystal formation in cells. Hungarian cultivars "Penzesdombi" and "Kiscsalai" are comparatively frost tolerant [231, 232]. Stem dieback has been reported in cold conditions, and frost can decrease growth rate and height.
Saccharum spp.	C4	Varies	Greatest ratoon cold tolerance was identified in *Saccharum spontaneum* genotypes IND 81–144, IND 81–80, IND 81–165, and MPTH 97–216, and these were more tolerant than the most tolerant commercial variety [233].
Salix spp.	C3	High	*Salix matsudana*, especially variety "Navajo," is extremely cold hardy [86]. With pretreatment (hardening), tropical willows were able to withstand cold temperatures (to −30 °C), while a northern willow (*Salix sieboldiana*), was able to withstand temperatures of −50 °C and survived immersion in liquid N at −196 °C after hardening for 2 weeks in cold temperatures [234].
Sorghastrum nutans	C4	Moderate	The base temperature for germination for *Sorghastrum nutans* was low to midrange (2.8 to 4.5 °C) among the warm-season grasses tested. Chilling symptoms were seen during chilling treatment for "Tomahawk," and in "Holt" after temperatures returned to normal. Leaf damage ranged from 30 % in Tomahawk (the lowest across all grasses) to 41 % for "Holt." Electrolyte leakage was among the lowest in "Tomahawk" for all grasses [214]. *Sorghastrum nutans* is not particularly cold tolerant, but var. "Lometa" had greater percent germination (24 %) at the low temperature treatment (5–15 °C) than other varieties (7–17 %) [87].

Table 4 (continued)

Taxa	Ps type	Tolerance level	Evidence of cold tolerance
Sorghum bicolor	C4	Low	*Sorghum bicolor* is sensitive to cold stress at all stages of development and typically is planted 3–5 weeks later than other annual crops to avoid inhibition of germination, emergence, and crop establishment [235]. Chilling (2–8 °C) for 1 to 8 days inhibited *Sorghum bicolor* growth and nitrogen uptake during exposure, and the ability to recover was greater in warmer and shorter chilling treatments [236]. Eight advanced breeding lines and one recombinant inbred line showed early emergence, higher biomass (30 days after emergence), and relatively earlier flowering than other lines under cold temperatures (14 °C) [237].
Spartina pectinata	C4	High	*Spartina pectinata* is known to have one of the most northerly distributions among C4 grasses [238]. Natural populations are found in the boreal forest of NW Canada where July mean minimum temperatures were greater than 7.5 °C [239], and cultivar CWNC was recommended for production in Canada due to early spring growth [240]. *Spartina pectinata* cells showed relatively limited injury under freezing conditions, possibly because, as a salt-marsh grass, it is salt tolerant and this may confer greater inherent cell freezing resistance [241].

response can halt the synthesis of other proteins [210] and cause oxidative stress [212]. Many heat-tolerant plants are able to maintain higher photosynthetic rates and membrane stability by increasing the proportion of saturated and mono-unsaturated fatty acids and maintain overall tissue water balance through osmotic adjustment [197]. A number of additional physiological changes occur in response to heat in tolerant taxa, including hormonal changes, increases in protective pigments, and synthesis of secondary metabolites. These are detailed, along with molecular tolerance mechanisms, in several comprehensive reviews [e.g., 196, 197, 199–201].

Heat- and Cold-Tolerant Biomass Crops

Several woody biomass crops are naturally cold tolerant (Table 4), as many of them evolved in cold climates, including alpine or boreal ecosystems. For example, the phenomenon of cellular "supercooling" is common among conifer species, and some *Pinus* species can survive temperatures as low as −196 °C [202]! Other cold-hardy woody crops include *Populus* [75, 227] and *Salix* spp. [86, 234] (Table 4), with *Robinia pseudoacacia* introduced into several Canadian provinces (http://plants.usda.gov/core/profile?symbol=rops). Moreover, in unpublished University of Illinois research, several hundred black locust genotypes survived the abnormally cold 2013–2014 winter in Urbana, IL (40.0645 N, −88.2078 W), when average January and February temperatures were 5.5 and 5.7 °C lower than 30-year averages; furthermore, all trees grew productively the following season (T. Voigt, personal observation). Several herbaceous biomass crops tolerate cold conditions, as well. These include *Spartina pectinata* [239, 241], as well as *Andropogon gerardii* cv. "Bison" [214], *Panicum virgatum* cv. "Dakota" [214] and other upland cytotypes [222], *Miscanthus sinensis* [242] and, to a lesser extent, *M.* × *giganteus* [60] (Table 4). Commonly cultivated *Panicum virgatum* cultivars "Alamo," "Cave-in-

Rock," and "Kanlow" were sensitive or moderately sensitive to low temperatures [243]. Although many *Agave* species are associated with warm desert ecosystems, a number of *Agave* spp. that evolved in high elevations (e.g., *Agave utahensis* and *Agave parryi*) are able to withstand temperatures down to −28 °C. In addition, cold-tolerant genotypes of subtropical and tropical biomass crops *Eucalyptus* spp. and *Saccharum* spp. have been developed (Table 4), indicating the possibility for cold tolerance to be improved in future breeding programs for these and other crops.

Because C4 and CAM species have inherent mechanisms to resist heat stress, it makes sense to consider biomass crops with these photosynthetic pathways (see Table 5). *Agave* species (CAM) can withstand temperatures between 57 and 65 °C because of thick cuticle, low absorbance of short-wave radiation, and deployment of heat shock proteins [244, 260]. A number of C4 and highly efficient C3 perennial grasses are heat tolerant, including *Andropogon gerardii*, *Arundo donax*, *Miscanthus sinensis*, and some *Sorghastrum nutans* and *Saccharum* varieties (Table 5). *Panicum virgatum* cultivars exhibit variable heat tolerance, with lowland cytotypes generally performing better in warm, southern climates [222]. For example, several *Panicum virgatum* genotypes show intermediate (cv. "Alamo" and others) to high tolerance (cv. "Summer") to heat stress during germination [243] and thus may be good candidates for production on marginal lands in warm regions. Commonly grown cultivars "Cave-in-Rock" and "Kanlow" were heat sensitive [243]. Heat-tolerant woody species include *Jatropha curcas*, and *Eucalyptus occidentalis* and others, *Pinus densiflora* and others, *Populus euphratica*, *Robinia pseudoacacia*, and *Salix nigra* (Table 5). Many of these crops evolved in hot climates, but others have been improved through breeding for greater heat tolerance. For example, a heat tolerant *Saccharum* spp. (CP-4333) has been developed and shows rapid recovery following heat stress [256 Table 5].

Table 5 Heat tolerance in 17 feedstocks with bioenergy potential

Taxa	Ps type	Tolerance level	Evidence of heat tolerance
Agave spp.	CAM	High	*Agave americana* produced the greatest levels of heat shock proteins in response to heat stress compared to three other moderately and highly heat tolerant species, protecting photosynthetic functioning [244].
Andropogon gerardii	C4	High	*Andropogon gerardii* photosynthetic components can tolerate high (35 °C+) temperatures, particularly under elevated CO_2 [245].
Arundo donax	C3	High	*Arundo donax* rhizome fragments can produce shoots and roots in controlled conditions up to 41 °C (R. Tayyar, L. Quinn, and J. Holt, unpublished data).
Eucalyptus spp.	C3	High	Several species (including *Eucalyptus deglupta*, *Eucalyptus pellita*, *Eucalyptus occidentalis*, and *Eucalyptus urophylla*) appear to be adapted to hot environments, based on conditions typical in their native range [53, 216]. *Eucalyptus occidentalis* leaves resist heat damage to 51.8 °C [216].
Helianthus annuus	C3	Low	High leaf temperatures (40–45 °C) were detrimental to physiological traits including photosynthetic rate, transpiration rate, and stomatal conductance [246]. Some genotypes can reduce heat load by changing leaf inclination, with the most tolerant genotypes angling leaves upward. These were able to maintain lower leaf temperatures and membrane leakage [247].
Jatropha curcas	C3	High	*Jatropha curcas* has a high tolerance for heat [157]. A period of heat treatment was favorable for young *Jatropha curcas* plants, unless heat was combined with salinity [159].
Miscanthus spp.	C4	Moderate	Heat shock genes have been identified in *Miscanthus sinensis* and could be used to improve future hybrids [248].
Panicum virgatum	C4	Moderate	Lowland cytotypes of *Panicum virgatum*, adapted to southern climates, may be more heat tolerant than upland types [223]. Even though plant height and total biomass decreased under heat stress [249], a climate modeling paper shows that *Panicum virgatum* yields could increase under warmer climate scenarios (3 to 8 °C), due to extended growing season and limited cold stress [211].
Pennisetum purpureum	C4		N/A
Pinus spp.	C3	High	*Pinus sylvestris* (20-year trees) increased in diameter earlier in the season and stopped growing later when exposed to elevated temperatures (compared with ambient temperatures), and diameter was 26 % greater in elevated temperatures vs ambient temperatures over the 3-year study [250]. Elevated temperatures did not significantly alter net photosynthesis across the native range of *Pinus taeda* [251]. *Pinus densiflora* relative growth rate and dry matter yield increased in response to higher temps (30 vs 25 °C) [252].
Populus spp.	C3	Varies	*Populus euphratica* is tolerant to extreme temperatures, via proteins related to lipid biogenesis, cytoskeleton structure, sulfate assimilation, thiamine and hydrophobic amino acid biosynthesis, and nuclear transport. Photosynthesis is maintained by decreasing photosystem II (PSII) abundance and increasing PSI contribution to linear electron flow [253].
Robinia pseudoacacia	C3	Moderate	Virginia Tech extension publication lists black locust as a heat tolerant tree, but recommends caution because of invasive tendencies [254]. Stem dieback was associated with hot, dry conditions in Oklahoma plantings [255].
Saccharum spp.	C4	Varies	A heat-tolerant variety of sugarcane (CP-4333) recovered more quickly from heat stress than a heat-sensitive variety, due to leaf rolling (decreased water loss) and rapid reversal of this effect during recovery [256].
Salix spp.	C3	Varies	*Salix arctica* responded negatively to simulated heat waves and did not recover its cold tolerance when normal (arctic) temperatures were reimposed [257]. *Salix phylicifolia*, which naturally occurs in or near natural hot springs in Iceland, had higher photosynthesis rates in hotter soils than in cool soils away from the hot springs [258]. *Salix nigra* plants treated with 40 °C hot water showed higher values both for photosynthesis rates and stomatal conductance than untreated plants [259].
Sorghastrum nutans	C4	Moderate	*Sorghastrum nutans* var. "Llano" and "Lometa" had a higher percent germination at the high temperature treatment (30–40 °C) than other varieties. Optimal temperatures for these were 10–30 °C ("Llano") and 15–30 °C ("Lometa") [87].
Sorghum bicolor	C4	Low	Heat stress significantly reduced glucose release and EtOH yield from hybrid DK-28E, especially during seed-filling stages [88].
Spartina pectinata	C4	Moderate	Relative *Spartina alterniflora* heat shock protein production in response to heat stress increased photosynthetic thermotolerance [244].

N/A no supporting evidence was found in literature databases

Additional Considerations in Evaluating Stress-Tolerant Biomass Crops

Multiple Stressors

While research into genetically modifying biofuel crops to enhance abiotic stress tolerance may expand the area suitable for cultivation [64], breeders will need to anticipate the combined stressors that are likely to occur in many marginal production systems. Different combinations of stressors may cause conflicting responses [261], but there are species that are well adapted to multiple stressors. For example, xerohalophytes are specialized halophytes (salt-tolerant species) that are found in dry conditions (e.g., *Salsola kali* [262]). Conversely, most true halophytes are adapted to wetlands and therefore have adaptations to withstand inundated *and* saline soils (e.g., *Spartina alterniflora* [263]). Some of these may be suitable for improvement as energy crops on marginal land. In contrast, multiple stressors often cause damage to growing plants, even if the plant is tolerant of a particular type of environmental stress. For example, *Jatropha curcas*, a highly heat-tolerant species, suffers more from the combination of salinity and heat stress than from either stressor alone [159]. Therefore, it will be important to identify the prevailing stressor(s) in the marginal area under production and choose the most tolerant biomass crops. It will also be important for producers to be aware of the possibility of reduced yield even among the most tolerant crops in years when multiple stressors occur (e.g., low rainfall years in saline conditions). Further, this review focused on a narrow, but physiologically important, set of stressors. We acknowledge that additional stress factors will influence biomass crop productivity on marginal land. Some of these, like nutrient deficiencies, can be ameliorated with available agronomic management practices.

Several of the crops we have highlighted are suitable for a number of stressful conditions. These will be discussed further in the "Conclusions" section.

Invasiveness

The ability to produce high biomass yields under unfavorable growing conditions is correlated with invasiveness, and several authors have cautioned against the use of non-native and potentially invasive biomass crops [264–270]. Some of the crops mentioned in this review have been evaluated as high-risk species and have received attention from environmental groups and invasion ecologists (e.g., *Arundo donax*, seed-bearing *Miscanthus* spp., *Jatropha curcas*, *Pennisetum purpureum*) [265, 267, 268, 271–275]. Therefore, these and other high invasion-risk crops should only be chosen when they can be grown and transported with strict containment procedures in place [276] and when state and federal regulations allow their introduction and cultivation [277, 278]. Other crops in this review, however, are either US natives or have been evaluated as low-risk for invasion in the USA [279]. The authors encourage the choice of native biomass crops, but note that most "native" species are only native to a specific region of the USA and can, in fact, be "weedy" or invasive outside of the native range (e.g., *Robinia pseudoacacia*, which is native to small areas in the Piedmont and Missouri regions, but has invaded and naturalized throughout the continental USA)

Table 6 Summary table of all species and all stressors

Taxa	Ps type	Drought	Flooding	Salinity	Heat	Cold
Agave spp.	CAM	High	No data	Varies	High	Varies
Andropogon gerardii	C4	High	No data	High	High	Moderate
Arundo donax	C3	Low	Moderate	High	High	Moderate
Eucalyptus spp.	C3	High	Varies	Varies	High	Varies
Helianthus annuus	C3	Nil	No data	Varies	Low	No data
Jatropha curcas	C3	High	Low	Moderate	High	Low
Miscanthus spp.	C4	Moderate	Moderate	Moderate	Moderate	Moderate
Panicum virgatum	C4	Low	Moderate	Moderate	Moderate	Moderate
Pennisetum purpureum	C4	High	No data	Low	No data	Low
Pinus spp.	C3	Varies	Varies	Varies	High	High
Populus spp.	C3	Varies	Varies	Varies	Varies	High
Robinia pseudoacacia	C3	High	No data	High (in 4n)	High	No data
Saccharum spp.	C4	Varies	Varies	Varies	Varies	Moderate
Salix spp.	C3	Varies	Varies	Moderate	Varies	High
Sorghastrum nutans	C4	Varies	No data	Varies	Moderate	Moderate
Sorghum bicolor	C4	High	Moderate	Varies	Low	No data
Spartina pectinata	C4	Low	High	High	Moderate	High

Source: [164]

[273]. In addition, some native species can be pests within their native regions. For example, *Helianthus annuus* is native to the entire continental USA but is a regulated noxious weed in Iowa due to its negative impacts on agriculture [277]. As such, it will be important for producers to choose biomass crops that are native and/or low-risk in the production region [279]. Growers can consult online databases to determine invasion risk [280–282] or choose from a recently released list of low-risk biomass crops [279].

Conclusions

Predicted climate changes will increase the likelihood of abiotic stress throughout the country, including various combinations of multiple stressors. For example, heat waves are predicted to become more intense throughout the country while precipitation is expected to increase in the northern USA and to decrease in the southwest [11]. Our literature review has revealed several "all purpose" biomass crops that are moderately or highly tolerant of multiple environmental stressors (Table 6). For example, *Andropogon gerardii*, *Eucalyptus* spp., *Miscanthus* spp., *Panicum virgatum*, *Pinus* spp., *Populus* spp., *Robinia pseudoacacia*, and *Spartina pectinata* were shown to be moderately or highly tolerant of four or more stress types. For particular growing conditions such as some hot and dry areas, growers could choose among *Agave americana*, *Andropogon gerardii*, *Jatropha curcas*, *Miscanthus sinensis*, *Pinus sylvestris*, *Pinus taeda*, *Populus euphratica*, or *Robinia pseudoacacia*. Many wet and saline environments could likely support *Arundo donax*, *Eucalyptus camaldulensis* (particularly *Eucalyptus camaldulensis* "Silverton" and "Local"), *Miscanthus × giganteus*, *Panicum virgatum* "Trailblazer," *Sorghum bicolor* varieties, and *Spartina pectinata*. Genera such as *Pinus* and *Populus* comprise a host of species that are adaptable to different stressors and combinations of stressors.

As previously mentioned, our list is not exhaustive and, in some cases, is based on studies that assessed relative—not absolute—stress tolerance, but it represents a much more comprehensive biomass crop selection guide for growers than currently exists. Based on this review, growers could choose from a variety of plant types representing a variety of industrial uses from ethanol (e.g., *Miscanthus* spp.) to combustion (e.g., *Pinus* spp.), depending on their preferences and the capabilities of local processing plants. In addition, we have indicated here that a number of biomass crops have already been improved for greater stress tolerance, and we assume that breeding programs will continue to develop additional stress-tolerant crops. Therefore, it appears that there will be a number of options available for marginal lands now and into the increasingly stressful future [105].

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