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Zuckerrübenanbau unter veränderten Klimabedingungen – Trockenstresstoleranz und Stickstoffnutzungseffizienz von Zuckerrübengenotypen

Zuckerrübenanbau unter veränderten Klimabedingungen

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Trockenstresstoleranz und Stickstoffnutzungseffizienz von Zuckerrübengenotypen

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Abkürzungsverzeichnis

ANOVA	Analysis of variance
BLE	Bundesanstalt für Landwirtschaft und Verbraucherschutz
BMJV	Bundesministerium der Justiz und für Verbraucherschutz
CGR	Crop growth rate
DM	Dry matter
DWD	Deutscher Wetterdienst
dps	Days past sowing
E	Environment
ED	Early drought
eq.	Equation
FM	Fresh matter
G	Genotype
H	Harvest date
ICUMSA	International Commission for Uniform Methods of Sugar Analysis
IPCC	Intergovernmental Panel on Climate Change
LD	Late drought
MD	Multiple drought
n.s.	not significant
N_{min}	Soil mineral nitrogen content
N_{supl}	Nitrogen supply
NUE/SNE	Nitrogen use efficiency/Stickstoffnutzungseffizienz
NUpE	Nitrogen uptake efficiency
N_{upt}	Nitrogen uptake
NUtE	Nitrogen utilization efficiency
p	Signifikanzwert
REML	Restricted maximum likelihood
RMSE	Root mean square error
RUE	Radiation use efficiency
SY	Sugar yield
t	Time
W	Water supply treatment
WHC/WHK	Water holding capacity/Wasserhaltekapazität
WUE/WNE	Water use efficiency/Wassernutzungseffizienz
WVZ	Wirtschaftliche Vereinigung Zucker
YSI	Yield stability index

Prolog

1 Auswirkungen klimatischer Veränderungen

Der Klimawandel ist eine weltweite Herausforderung für gesellschaftliche, politische und wirtschaftliche Systeme (Dryzek et al. 2011). Ein Wirtschaftsbereich mit besonders starker Abhängigkeit von den Wetter- und Klimabedingungen ist die Landwirtschaft. Aufgrund der klimatischen Veränderungen wird in Zukunft eine Reduktion in der Häufigkeit und Intensität von Sommerniederschlägen erwartet (IPCC 2013). Trockenstress als Folge von Wassermangel wird als einer der wichtigsten Stressfaktoren betrachtet (Shao et al. 2009) und beeinträchtigt Wachstum und Entwicklung von Pflanzen. Anhand von Isotopenuntersuchungen in Baumringen stellten Büntgen et al. (2021) fest, dass in Zentraleuropa in den Jahren 2015-2018 eine im Vergleich zu den letzten 2100 Jahren beispiellose Dürreperiode aufgetreten ist. In Deutschland war die Niederschlagsmenge in den Sommermonaten 2018 im Vergleich zum fünfjährigen Mittel der Vorjahre um 46 % verringert (DWD 2019). Im selben Jahr waren auch die Erträge von Getreide, Mais und Zuckerrüben deutlich reduziert (WVZ 2019; Statista 2019). Die Trockenheit war vermutlich die maßgebliche Ursache dafür, dass die Pflanzen nicht ihr volles Ertragspotential ausschöpfen konnten.

Bei Wassermangel ist auch die Verfügbarkeit von Nährstoffen begrenzt, weil der Nährstofffluss hin zu den Wurzeln sowie die Nährstoffaufnahme durch die Pflanzen vermindert ist (Ehlers und Goss 2003). Stickstoff als essentieller Nährstoff wird dabei als einer der mengenmäßig wichtigsten Nährstoffe betrachtet (Maathuis und Diatloff 2013). Daher wird bei Wassermangel die Ertragsbildung auch durch eine limitierte Stickstoffverfügbarkeit begrenzt (Sinclair und Rufty 2012).

Das volle Ertragspotential kann nur ausgeschöpft werden, wenn eine Sorte unter optimalen Wachstumsbedingungen angebaut wird und es keine Limitierung der Wasser- und Nährstoffversorgung gibt, sowie eine effektive Kontrolle von Krankheiten, Schädlingen, Unkräutern und anderen Stressfaktoren sichergestellt ist (Evans und Fischer 1999). Um in Zukunft eine steigende Weltbevölkerung mit Lebens- und Futtermitteln versorgen zu können, muss die landwirtschaftliche Produktion nachhaltig gesteigert, vor allem aber auch an die klimatischen Veränderungen angepasst werden. Neben der Verbesserung des

Anbaumanagements und der Reduzierung von Ernteverlusten zählt dazu auch die züchterische Anpassung und Verbesserung von Sorten (Meyer et al. 2013).

Zuckerrüben sind im Vergleich zu anderen Fruchtarten effizient in der Nutzung von Ressourcen (Hoffmann und Stockfisch 2010). Dennoch wird in Zukunft aufgrund veränderter klimatischer Bedingungen eine eingeschränkte Verfügbarkeit von Wasser und Stickstoff erwartet, sodass auch bei Zuckerrüben die Ertragsbildung beeinträchtigt wird (Pidgeon et al. 2001; Sinclair und Rufty 2012; Lipiec et al. 2013). Zusätzliche Wassergaben durch Beregnung sind nicht in allen Regionen möglich. Ebenso sind die Kontingente zur Wasserentnahme häufig limitiert (Elliott et al. 2014). Auch unbegrenzt zusätzliche Düngergaben sind nicht möglich und auch nicht wünschenswert, weil zu hohe Düngermengen zu Beeinträchtigungen der Umwelt führen (Mosier 2001; Galloway et al. 2003). Deshalb fordert auch die Gesetzgebung einen nachhaltigen und ressourceneffizienten Einsatz von Nährstoffen (BMJV 2009). Aus diesem Grund gilt es zu prüfen, ob genetische Unterschiede in der Nutzungseffizienz von Wasser und Nährstoffen dabei helfen könnten, die Ressourceneffizienz in der Zuckerrübenproduktion noch weiter zu steigern. Untersuchungen von Loel (2014) zufolge hat die Züchtung mit einem Anteil von 50 % großes Potential, Ertrag und Qualität von Zuckerrüben zu verbessern. Um Zuckerrüben züchterisch an veränderte Klimabedingungen anzupassen, ist ein tiefgreifendes Verständnis über genotypische Unterschiede in der Reaktion von Zuckerrüben auf Trockenstress und unterschiedliches Stickstoffangebot notwendig. Daher soll im ersten Teil der vorliegenden Arbeit zunächst der Effekt von Trockenstress bei Zuckerrüben und im zweiten Teil die Reaktion auf ein unterschiedliches Stickstoffangebot untersucht werden.

2 Trockenstresstoleranz

2.1 Reaktion von Zuckerrüben und anderen Fruchtarten auf Trockenstress

Wasser ist für viele Prozesse in der Pflanze, wie die CO_2-Assimilation, biochemische Umsetzungsprozesse oder den Stofftransport, von großer Bedeutung und somit wichtig für das Pflanzenwachstum (Ehlers und Goss 2003). Vor allem im Sommer nimmt mit steigenden Lufttemperaturen das Sättigungsdefizit der Atmosphäre zu, was zu einer Erhöhung des Wasserbedarfs der Pflanzen führt (Sinclair und Weiss 2010). Wenn bei der Transpiration die Abgabe von Wasser über die Blätter die Wasseraufnahme aus dem Boden übersteigt, erfahren Pflanzen Trockenstress (Tezara et al. 1999). Dies zeigt sich in der Pflanze als erstes in einer Reduktion des Wasserpotentials in den Blättern, das zu einer Abnahme des Turgordrucks in den Schließzellen, die die Stomata umgeben, führt. Dadurch werden die Stomata geschlossen und der Verlust von Wasser durch Transpiration reduziert (Pinheiro und Chaves 2011). Infolgedessen kommt es auch zu einer Reduktion der Photosynthese aufgrund eingeschränkter CO_2-Aufnahme und einer Hemmung des CO_2-Metabolismus (Tezara et al. 1999; Lawlor und Cornic 2002). Ebenso ist bei geschlossenen Stomata die Nährstoffaufnahme und der Transport von Assimilaten aufgrund des fehlenden Massenflusses eingeschränkt, sodass Photosynthese und Trockenmasseproduktion zusätzlich beeinträchtigt werden (Dunham und Clarke 1992).

Die Auswirkungen von Trockenstress sind abhängig von der Stärke, der Dauer und der Reaktion der Pflanzen nach einem Trockenstressereignis, sowie der Wachstumsphase, in der der Trockenstress auftritt (Demirevska et al. 2009). Insbesondere während Blüte und Kornfüllung kann eine durch Trockenstress verursachte Beeinträchtigung der Enzymaktivität sowie des Assimilatflusses innerhalb der Pflanze Auswirkungen auf die Ertragsbildung haben (Farooq et al. 2009). Speziell bei Getreide und Mais führt dies zu weniger und kleineren Körnern, sodass diese Fruchtarten in diesen Wachstumsphasen besonders anfällig für Trockenheit sind (Samarah 2005; Monneveux et al. 2006).

Grundsätzlich haben Pflanzen verschiedene morphologische, physiologische und biochemische Mechanismen der Anpassung entwickelt, um Phasen mit Trockenstress überstehen zu können (Bohnert et al. 1995). Diese Anpassungen können untergliedert werden in Trockenstressflucht (drought escape), Trockenstressvermeidung (drought avoidance) und Trockenstressanpassung (drought tolerance). Trockenstressflucht ist gekennzeichnet durch schnelles Wachstum und eine frühe Blüte, um den gesamten Lebenszyklus vor dem endgültigen Einsetzen von Trockenstress abzuschließen. Bei der Trockenstressvermeidung wird der Wasserverlust durch Transpiration begrenzt und die Aufnahme von Wasser möglichst aufrechterhalten. Trockenstressanpassung ist die Fähigkeit von Pflanzen, sich an einen niedrigen Wassergehalt im Gewebe anzupassen und durch Mechanismen zur Aufrechterhaltung des Turgors den Wassermangel zu ertragen (Farooq et al. 2009; Aslam et al. 2015; Kooyers 2015; Ilyas et al. 2021).

2.1.1 Trockenstressflucht

Bei der Trockenstressflucht handelt es sich um eine Anpassung, bei der die Pflanzen sich schnell entwickeln, sodass der gesamte Lebenszyklus verkürzt wird. Dies ermöglicht es, das generative Wachstum vor dem Auftreten eines Trockenstressereignis abzuschließen (Araus et al. 2002; Aslam et al. 2015; Kooyers 2015). Daher sind ein früher Blütezeitpunkt und eine frühe Reife wichtige Merkmale von Genotypen, die vor allem an Umwelten angepasst sind, in denen die Vegetationsperiode durch das Auftreten von Trockenstress verkürzt ist (Farooq et al. 2009).

In Australien konnte beobachtet werden, dass Weizensorten mit einer früheren Blüte und Reife einen Ertragsvorteil bei Trockenstress hatten, weil die anfälligen Wachstumsstadien früher durchlaufen wurden (Richards et al. 2014). Auch bei Mais (Ngugi 2013) und Kirchererbsen (Kumar und Abbo 2001) gibt es genotypische Variation im Blütezeitunkt. Diejenigen Genotypen, die eine frühere Blüte zeigen, haben ihre Entwicklung bereits vor dem gewöhnlichen Auftreten von Trockenstress abgeschlossen. Dadurch können Ertragsverluste reduziert und somit eine Anpassung an Trockenstressumwelten erzielt werden. Dies zeigt, dass genotypische Variation im Blütezeitpunkt bei verschiedenen Fruchtarten vorhanden ist und somit die Möglichkeit besteht, Trockenstressflucht züchterisch zu nutzen.

Zuckerrüben hingegen werden im kommerziellen Anbau bereits im vegetativen Wachstum geerntet. Im Vergleich zu anderen Fruchtarten muss daher zur Entwicklung des Ernteproduktes nicht die generative Wachstumsphase durchlaufen werden, sodass bei Zuckerrüben auch keine trockenheitsanfälligen Wachstumsstadien wie Schossen oder Blüte vorkommen (Dunham 1993). Aus diesem Grund können genotypische Unterschiede im Blütezeitpunkt bei Zuckerrüben keine Auswirkungen auf die Anpassung an Trockenstressbedingungen haben.

2.1.2 Trockenstressvermeidung

Zu der Trockenstressvermeidung zählen Anpassungen von Pflanzen, durch die bei Trockenheit der Wasserverlust durch Transpiration vermindert und die Wasseraufnahme aufrechterhalten wird (Turner et al. 2001; Kavar et al. 2008). Insbesondere Blätter und Wurzeln sind von Trockenstress betroffen und können daher Bestandteil dieser pflanzlichen Anpassung sein. Dabei können beispielsweise die Oberflächenbeschaffenheit, das Einrollen, sowie Anzahl und Größe der Blätter, die Leitfähigkeit der Stomata oder auch Anpassungen im Wurzelsystem zur Vermeidung von Trockenstress beitragen (Farooq et al. 2009; Aslam et al. 2015). Genotypische Unterschiede in der Beschichtung der Blätter mit Wachs führte bei Weizen zu Unterschieden in der Wassernutzungseffizienz und in der Blattseneszenz. Die

Auswirkungen auf den Ertrag waren aber letztendlich sehr gering (Richards et al. 1986). Auch in der stomatären Leitfähigkeit zeigten sich genotypische Unterschiede bei Sojabohnen (Gilbert et al. 2011) und Gerste (González et al. 1999), die zu Unterschieden zwischen den Genotypen in der Wassernutzungseffizienz (WNE) bzw. im Ertrag führten. Bei Maispflanzen ist als Reaktion auf Trockenstress ein Einrollen des Blattes und eine Änderung des Neigungswinkels zu beobachten, um die dem Sonnenlicht ausgesetzte Fläche zu reduzieren. Dadurch kann die Transpiration und somit der Wasserverlust verringert werden (Baret et al. 2018). Im Beginn und der Intensität des Einrollens gibt es genotypische Unterschiede, die dazu führen, dass der Wassergehalt der Blätter unterschiedlich ist (Effendi et al. 2019).

Neben den Anpassungen der Blätter zur Reduktion des Wasserverlustes kann ebenso ein tiefreichendes Wurzelsystem dazu beitragen, Trockenstressphasen zu überstehen (Farooq et al. 2009). Bei Mais (Hund et al. 2009), Soja (Fried et al. 2019), Reis (Kato et al. 2006) und Sorghum (Ludlow et al. 1990) konnten genotypische Unterschiede in der Durchwurzelungstiefe festgestellt werden, die es ermöglichen, Wasserreserven in tieferen Bodenschichten zu erschließen und die Ertragsbildung unter Trockenstress zu verbessern. Diese Beispiele zeigen, dass es bei verschiedenen Fruchtarten genotypische Variation in Blatt- und Wurzelmerkmalen gibt, die zur Trockenstressvermeidung beitragen können.

Auch bei Zuckerrüben ermöglicht ein tiefreichendes Wurzelsystem, bei Trockenheit Wasser in tieferen Bodenschichten zu erschließen und somit das Auftreten von Trockenstress zu vermeiden (Scott und Jaggard 1993; Morillo-Velarde und Ober 2006). Allerdings beginnt die Ausbildung von Wurzeln in diese tieferen Bodenschichten und die anschließende aktive Wasseraufnahme erst mit einer Verzögerung von 16 Tagen nach dem Auftreten von Trockenstress (Fitters et al. 2017, 2018). Zudem trägt die Wasseraufnahme aus tieferen Bodenschichten nur in begrenzten Umfang zum Gesamtwasserverbrauch bei (Brown und Biscoe 1985). Daher ist fraglich, inwiefern das Wurzelsystem bei Zuckerrüben zu einer verbesserten Trockenstresstoleranz beitragen kann.

2.1.3 Trockenstressanpassung

Trockenstressanpassung beschreibt die Fähigkeit von Pflanzen, sich in bestimmten Merkmalen an einen Wassermangel anzupassen und dadurch Wachstum und Ertragsbildung trotz Trockenstress aufrechtzuerhalten (Ehlers und Goss 2003; Aslam et al. 2015). Verschiedene Stoffe und Prozesse sind aktiv an der Trockenstressanpassung beteiligt.

Phytohormone regulieren das Schließen der Stomata in Reaktion auf Wassermangel, sodass der Wasserverlust durch Transpiration reduziert werden kann (Yürekli et al. 2001). Antioxidative Abwehrmechanismen können in Reaktion auf Trockenstress aktiviert werden, um Zellwand- und Membranstrukturen vor oxidativen Schäden in Folge von Trockenstress zu schützen (Aslam et al. 2015; Maqbool et al. 2017). Die osmotische Anpassung ist ein weiterer wichtiger Prozess, um die Auswirkungen von Wassermangel zu reduzieren. Durch Anreicherung von osmotisch aktiven Substanzen in den Zellen kann das osmotische Potential abgesenkt werden und damit ein Abfall des Turgordrucks verhindert werden (Ludlow 1987; Schopfer und Brennicke 2006; Blum 2017). Dadurch können trotz Wassermangel physiologische Prozesse wie der Gasaustausch und damit die Photosynthese und das Wachstum aufrechterhalten werden (Oosterhuis und Wullschleger 1987; Chaves und Oliveira 2004). Die osmotische Anpassung ermöglicht ebenso eine bessere Verlagerung von Assimilaten in die Speicherorgane (Subbarao et al. 2000).

Genotypische Unterschiede in der osmotischen Anpassung konnten bei vielen verschiedenen Fruchtarten, u.a. Gerste (González et al. 2008), Weizen (Moinuddin et al. 2005) und Mais (Chimenti et al. 2006), beobachtet werden. Obwohl es einen allgemeinen Zusammenhang zwischen der osmotischen Anpassung und dem Ertrag unter Trockenstress gibt (Blum 2017), wird die Rolle bei der Aufrechterhaltung von Wachstum und Ertragsbildung unter Trockenstress kritisch diskutiert (Turner 2018).

Auch Zuckerrüben reagieren mit osmotischer Anpassung auf Trockenstress. Dabei verfügt aber im Gegensatz zur kultivierten Form der Zuckerrübe *Beta vulgaris* vor allem die Wildform *Beta maritima* über wirksame Mechanismen zur Anreicherung von osmotisch aktiven Substanzen bei Trockenstress (Bagatta et al. 2008). Es wird aber vermutet, dass die generelle Variabilität innerhalb der Gattung *Beta* im Vergleich zu anderen Fruchtarten gering ist, sodass die Möglichkeit der Nutzbarmachung von osmotischer Anpassung durch die Züchtung bei Zuckerrüben begrenzt scheint (Hoffmann et al. 2020).

2.2 Aktueller Stand der Forschung zur Trockenstresstoleranz bei Zuckerrüben

In Zukunft wird ein verstärktes Auftreten von Trockenstressperioden erwartet. Dies macht es auch für Zuckerrüben erforderlich, die Effizienz in der Wassernutzung zu erhöhen und mögliche trockenstresstolerante Genotypen zu identifizieren. Zuckerrüben benötigen nur etwa 200 L Wasser, um 1 kg Gesamttrockenmasse zu bilden. Sie sind damit im Vergleich zu anderen Fruchtarten eher effizient in der Wassernutzung und bereits gut an Trockenheit angepasst (Ehlers und Goss 2003). Die WNE beschreibt dabei die Gesamttrockenmasse oder auch den Zuckerertrag in Beziehung zum Wasserverbrauch (Boyer 1996).

In verschiedenen Studien wurde die Reaktion von Zuckerrüben auf Trockenstress bereits untersucht, um Erkenntnisse für mögliche züchterische Verbesserungen der Trockentoleranz oder einer effizienteren Wassernutzung zu erlangen. In Versuchen mit künstlich durch Folientunnel erzeugtem Trockenstress trat Variation in der physiologischen Reaktion (Welkegrad, Einzelblattgewicht, Sukkulenzindex, Chlorophyllgehalt in alten Blättern) auf, aber es gab keine Zusammenhänge der Merkmale mit dem Ertrag (Chołuj et al. 2014). In anderen Untersuchungen an einem breiten Set mit Zuckerrübengenotypen aus züchterisch unbearbeitetem Genmaterial trat nur wenig Variation in der Trockentoleranz auf (Ober und Luterbacher 2002; Ober et al. 2004). Genotypische Unterschiede traten dabei lediglich in Blattmerkmalen auf, hingegen gab es keine Variation bei Merkmalen mit engem Bezug zur Ertragsbildung wie Photosyntheserate oder Wasserverbrauch. Zudem waren die Erträge unter Trockenstress eng gekoppelt an die Erträge unter Bewässerung (Ober und Luterbacher 2002; Ober et al. 2004; Ober et al. 2005), was eher auf eine fehlende genotypische Trockenstresstoleranz hindeuten würde. Trockenstressversuche im Gewächshaus mit einem kleinen, eher ähnlichen Genotypenset zeigten ähnliche Ergebnisse. Eine fehlende Interaktion zwischen Genotyp und Wasserversorgung für Trockenmasseproduktion und WNE deutete ebenso darauf hin, dass es bei Zuckerrüben keine spezielle Anpassung an Trockenstress gibt (Bloch et al. 2006b).

Trotz dieser Erkenntnisse wird die genotypische Trockenstresstoleranz bei Zuckerrüben weiterhin diskutiert. Es ist nicht bekannt, ob Zuckerrüben eine Wachstumsphase mit höherem Wasserbedarf und entsprechend stärkerer Anfälligkeit für Trockenstress besitzen. In einer solchen Phase kann ein stärkerer Trockenstresseffekt und folglich genotypische Variation in der Reaktion erwartet werden. Die Kenntnis über das Auftreten einer solchen Wachstumsphase könnte für die Züchtung von Bedeutung sein, um gezielt in einer bestimmten Wachstumsphase auf Trockentoleranz selektieren zu können. Wie in Kapitel 2.1 beschrieben, gibt es für andere Fruchtarten genotypische Variation bei Merkmalen mit Bezug zur Trockenstresstoleranz und somit Möglichkeiten, gezielt bei der Züchtung auf bestimmte Merkmale zu selektieren. Bei Zuckerrüben hingegen ist weiterhin nicht klar, anhand welcher Merkmale Genotypen selektiert werden sollten, damit sie möglicherweise eine Trockentoleranz besitzen oder zumindest effizient in der Wassernutzung sind, um unter Bedingungen mit begrenzter Wasserversorgung möglichst hohe Erträge erzielen zu können.

2.3 Ziele der Arbeit – Trockenstress

Durch die klimatischen Veränderungen mit vermehrtem Auftreten von Trockenstressperioden werden in Zukunft stärkere Beeinträchtigungen bei der Ertragsbildung von Zuckerrüben erwartet. Um an diese Bedingungen angepasste Sorten entwickeln zu können, ist ein größeres Verständnis über die Reaktion von Zuckerrüben auf Trockenstress notwendig.

In dieser Arbeit soll daher unter kontrollierten Bedingungen im Gewächshaus untersucht werden, in welcher Wachstumsphase der Wasserbedarf von Zuckerrüben am größten und daher die Reaktion auf Trockenstress am stärksten ist. Es soll außerdem geprüft werden, auf welches Merkmal selektiert werden könnte, um Genotypen zu erhalten, die unter Bedingungen mit Trockenstress und wechselnder Wasserversorgung in der Ertragsleistung überlegen sind.

In Feldversuchen soll die Reaktion auf unterschiedliche Umwelteinflüsse, insbesondere Trockenstress unter natürlichen Bedingungen, untersucht werden. Dabei soll analysiert werden, wie sich die Ertragsstabilität, aber auch das Verhältnis von Rübenertrag und Zuckergehalt unter Trockenstress bei unterschiedlichen Genotypen verhält. Ferner soll geprüft werden, unter welchen Bedingungen an Trockenheit angepasste Genotypen selektiert werden sollten.

3 Stickstoffnutzungseffizienz

3.1 Reaktion von Zuckerrüben und anderen Fruchtarten auf unterschiedliches Stickstoffangebot

Die Verfügbarkeit von Stickstoff im Boden kann von verschiedenen Faktoren wie der Feuchtigkeit und Temperatur im Boden, aber auch vom Bodentyp und pH-Wert beeinträchtigt werden (Masclaux-Daubresse et al. 2010). Ebenso kann das Stickstoffangebot vermindert sein, weil Verluste durch Auswaschung ins Grundwasser oder als Emission in die Atmosphäre auftreten, was zusätzlich eine Belastung der Umwelt darstellt (Mosier 2001; Galloway et al. 2003). Die Effizienz, mit der Stickstoff von den Pflanzen aufgenommen und genutzt wird, kann mit der Stickstoffnutzungseffizienz (SNE) beschrieben werden. Diese setzt sich zusammen aus der Effizienz, Stickstoff aus dem Boden aufzunehmen (Aufnahmeeffizienz) und der Fähigkeit, den aufgenommenen Stickstoff zu verwerten (Verwertungseffizienz) (Moll et al. 1982).

Genotypische Unterschiede in der SNE gibt es bei verschiedenen Fruchtarten wie Weizen (Ortiz-Monasterior et al. 1997; Wang et al. 2011; Latshaw et al. 2016), Gerste (Anbessa et al. 2009), Mais (Coque und Gallais 2007), Raps (Berry et al. 2010) und auch Reis (Souza et al. 1998; Zhang et al. 2009). Dabei ist nicht eindeutig geklärt, ob die Stickstoffaufnahme- oder die Verwertungseffizienz einen größeren Einfluss auf die SNE hat. Es wurde aber bei vielen Fruchtarten beobachtet, dass bei geringem Stickstoffangebot die Stickstoffaufnahmeeffizienz, bei hohem Stickstoffangebot dagegen die Stickstoffverwertungseffizienz wichtiger ist (Ortiz-Monasterior et al. 1997; Coque und Gallais 2007; Anbessa et al. 2009; Berry et al. 2010).

Bei der Aufnahme von Stickstoff aus dem Boden ist das Wurzelsystem von besonderer Bedeutung. Bei Weizen konnten genotypische Unterschiede in der Wurzeltrockenmasse beobachtet werden, aus denen auf Unterschiede in der Ausprägung des Wurzelsystems geschlossen wurde (Wang et al. 2011). Dabei soll ein stärker ausgeprägtes Wurzelsystem eine bessere Stickstoffaufnahme aus dem Boden ermöglichen, sodass Wachstum und Ertragsbildung verbessert sind und folglich auch eine höhere SNE erzielt wird (Bengough et al. 2006). Auch bei Raps wiesen Genotypen mit einer höheren SNE ein stärkeres Wurzelwachstum auf (Kamh et al. 2005). Grundsätzlich ist es möglich, dass es auch bei Zuckerrüben genotypische Variation im Wurzelwachstum gibt. Jedoch sind Zuckerrüben gerade zu Beginn des Wachstums in der Lage, den Stickstoff aus dem Boden nahezu komplett aufzunehmen (Armstrong et al. 1986). Daher ist es fraglich, ob mit Hilfe einer Verbesserung des Wurzelsystems die SNE von Zuckerrübengenotypen weiter verbessert werden kann, wenngleich dieser Einflussfaktor auch nicht komplett ausgeschlossen werden kann.

Bei Raps und Mais konnte beobachtet werden, dass ein höherer Ertrag bei geringem Stickstoffangebot mit der Stickstoffaufnahme nach der Blüte in Zusammenhang steht (Berry et al. 2010; Ciampitti und Vyn 2012). Zur Bestimmung von genotypischen Unterschieden im Ertrag waren Unterschiede in der Stickstoffaufnahme in dieser Phase am wichtigsten, sodass dieses Merkmal bei der Identifizierung von Genotypen mit hohem Ertrag bei geringem Stickstoffangebot (hohe SNE) helfen könnte. Für die Verbesserung der SNE von Zuckerrüben spielt das jedoch keine Rolle, weil Zuckerrüben bereits im vegetativen Wachstum geerntet werden und daher kein Blütestadium vorkommt.

Die Verwertungseffizienz als Bestandteil der SNE wird insbesondere in der reproduktiven Wachstumsphase durch die Verlagerung von Stickstoff beeinflusst. Genotypische Variation in der Stickstoffmenge, die von Stängel oder Blättern in die Körner verlagert wird, zeigt sich bei Raps (Schjoerring et al. 1995; Malagoli et al. 2005), Mais (Coque und Gallais 2007) oder Weizen (Wang et al. 2011). Auch bei Reis korreliert der Kornertrag mit der Effizienz, mit der der aufgenommene Stickstoff in die Körner verlagert wird. Daraus wird geschlossen, dass eine hohe Senkenstärke (sink strength) an der Verwertungseffizienz und damit auch an der SNE beteiligt ist (Ntanos und Koutroubas 2002). Genotypische Variation in der Rispenanzahl führte dabei zu geringerem Stickstoffbedarf bei der Kornfüllung und somit zu einer geringeren Senkenstärke, womit Unterschiede in der SNE von Reis erklärt wurden (Zhang et al. 2009). Im Vergleich zu diesen Fruchtarten enthält bei Zuckerrüben das Haupternteprodukt kaum Stickstoff, sondern nahezu ausschließlich Zucker, welcher mit etwa 75 % den Hauptbestandteil der Rübentrockenmasse darstellt (Hoffmann et al. 2005). Dies kann auf eine geringere genotypische Variation im Stickstoffbedarf und damit auch in der SNE bei Zuckerrüben hindeuten.

Dennoch ist auch bei Zuckerrüben eine ausreichende Stickstoffversorgung wichtig für Wachstum und Ertragsbildung. Dabei wird Stickstoff weniger eine Bedeutung bei der Speicherung von Zucker in der Rübe (Sink), sondern eher dem Blattwachstum zugeordnet (Source) (Hoffmann et al. 2020). Daher verlangsamt eine eingeschränkte Stickstoffversorgung das Blattwachstum (Milford et al. 1985), führt zu geringen Chlorophyllgehalten in den Blättern, was anhand der Blattfärbung sichtbar wird. Eine dadurch beschleunigte Blattseneszenz schränkt die Strahlungsabsorption und somit auch die

Photosynthese ein und hat damit Auswirkungen auf die Ertragsbildung (Draycott und Christenson 2003; Malnou et al. 2008). Ob dabei Variation in der Blattfärbung als Reaktion auf ein unterschiedliches Stickstoffangebot in Beziehung zum Zuckerertrag steht und damit auf genotypische Unterschiede in der SNE hindeuten kann, ist nicht geklärt. Eine zu hohe Stickstoffversorgung hingegen führt zu geringeren Zuckergehalten und einer starken Anreicherung von Amino-N in der Rübe, wodurch die Verarbeitungsqualität beeinträchtigt wird (Pocock et al. 1990; Jaggard et al. 2009a). Ebenso wird durch eine übermäßige Stickstoffversorgung die Trockenmasseverteilung in Richtung Blattwachstum und Zellwandbestandteile verschoben, ohne die Gesamttrockenmasse zu erhöhen (Milford et al. 1988; Laufer und Koch 2017). Ob es dabei genotypische Unterschiede gibt und durch eine optimierte Aufteilung der Trockenmasse die SNE möglicherweise verbessert werden kann, ist nicht bekannt. Beim Vergleich von Zucker- und Futterrüben konnte eine verbesserte Stickstoffnutzungseffizienz mit höheren Zuckererträgen erklärt werden (Laufer und Koch 2017). Unterschiede zwischen Genotypen in Stickstoffaufnahme und Verwertungseffizienz wurden bisher nicht umfassend untersucht.

3.2 Ziele der Arbeit – Stickstoffversorgung

Neben der Ressource Wasser sollte auch die Ressource Stickstoff von Zuckerrüben effizient genutzt werden. Aufgrund klimatischer Veränderungen könnte das Stickstoffangebot in Zukunft häufiger begrenzt sein. Daher werden im zweiten Teil dieser Arbeit die Komponenten der SNE bei Zuckerrüben untersucht und Ursachen für eine genotypische Variation analysiert. Es soll geprüft werden, hinsichtlich welcher Merkmale in der Sortenentwicklung selektiert werden sollte, um die SNE verbessern zu können. Da Stickstoff hauptsächlich die Blattbildung von Zuckerrüben fördert, soll auch die Bedeutung des Blattes für die Ertragsbildung sowie die Assimilatverteilung zwischen Sink und Source untersucht werden.

4 Aufbau der Arbeit

Die Ergebnisse der Untersuchungen der vorliegenden Arbeit wurden in Form von drei eigenständigen Manuskripten in wissenschaftlichen Journalen bereits veröffentlicht.

Manuskript I:

HENNING EBMEYER AND CHRISTA M. HOFFMANN, 2022: Water use efficiency of sugar beet genotypes: A relationship between growth rate and water consumption. Journal of Agronomy and Crop Science 208, 28-39, DOI: 10.1111/jac.12569.

Manuskript II:

HENNING EBMEYER, KARIN FIEDLER-WIECHERS, CHRISTA M. HOFFMANN, 2021: Drought tolerance of sugar beet – Evaluation of genotypic differences in yield potential and yield stability under varying environmental conditions. European Journal of Agronomy 125, DOI: 10.1016/j.eja.2021.126262.

Manuskript III:

HENNING EBMEYER AND CHRISTA M. HOFFMANN, 2021: Efficiency of nitrogen uptake and utilization in sugar beet genotypes. Field Crops Research 274, DOI: 10.1016/j.fcr.2021.108334.

Für die Möglichkeit der Nutzung der Manuskripte in dieser Arbeit möchte ich mich an dieser Stelle recht herzlich bei den Verlagen Elsevier und Wiley-Blackwell bedanken.

Im Epilog dieser Arbeit werden abschließend die Erkenntnisse aus den einzelnen Untersuchungen zusammenfassend betrachtet. Dabei soll aufgezeigt werden, welche Merkmale zukünftige Zuckerrübensorten aufweisen sollten, um effizient vorhandene Ressourcen zu verwenden.

Manuskript I

Water use efficiency of sugar beet genotypes: A relationship between growth rate and water consumption[1]

HENNING EBMEYER, CHRISTA M. HOFFMANN

Abstract

Drought stress restricts sugar beet growth and yield formation. For the development of adapted varieties, reasons for high water demand in certain growth periods and for genotypic differences in water use efficiency (WUE) were investigated. In 2019 and 2020, different drought stress periods were simulated in pot trials in the greenhouse with four sugar beet genotypes by reducing the water supply to 50% of the water holding capacity. With unlimited water supply, water consumption developed in parallel to the growth rate. This indicates that water demand is driven by growth rate. Therefore, early drought stress in the period with highest growth rate caused strongest yield reductions, which could not be compensated later in the season. Unlike sugar yield, water consumption differed among genotypes, resulting in genotypic differences in WUE. However, no relevant genotype by water supply interaction occurred, giving no indication for drought tolerance of the genotypes with high WUE. WUE is rather determined by the sugar yield potential of a genotype than by water supply. Therefore, sugar beet genotypes should be selected for their sugar yield potential when breeding for environments with varying water supply.

Keywords

abiotic stress, drought, sink, source, water supply, WUE

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[1] Ebmeyer and Hoffmann, 2022: Water use efficiency of sugar beet genotypes: A relationship between growth rate and water consumption. Journal of Agronomy and Crop Science 208, 28-39, DOI: 10.1111/jac.12569.

1 Introduction

Climatic changes are expected to lead to an increase in frequency and intensity of drought in the future and thus to periods of water shortage (IPCC, 2013). In Central Europe, the recent succession of summer drought periods (2015-2018) is in its extent unprecedented compared to the last 2100 years (Büntgen et al., 2021). However, water is a fundamental prerequisite for the development and growth of plants. Likewise, sugar beet yield formation is strongly dependent on water uptake (Jaggard et al., 2007; Jaggard et al., 2010). There is evidence that the demand for resources such as water is determined by the growth rate (White et al., 2016).

The growth rate changes during growth and is highest for sugar beet earlier in the season (Hoffmann et al., 2020). For sugar beet, the relationship between water consumption and growth rate, as well as the development of growth rate during different periods of drought stress, has not yet been comprehensively studied.

Sugar beet growth rate has often been determined by the yield increment between two sequential harvest dates (Bloch & Hoffmann, 2005; Kenter et al., 2006). However, this is a destructive approach and furthermore, it cannot reflect the exact changes at any time point in longer harvest intervals, especially when growth is disturbed by stress. A non-destructive method could be a solution to study growth and impact of abiotic stress throughout the entire growing season.

One option for non-destructive analysis of growth could be the phenotyping with sensor technologies as described for cereals (Hassan et al., 2019; Raeva et al., 2019), maize (Tirado et al., 2020; Tumilsa, 2017), or cotton (Feng et al., 2020). This is based on the observation that there is a close relationship between light interception and thus leaf canopy and yield, which exists for many crops in the absence of any stresses (Board et al., 1992; Edwards et al., 2005; Khurana & McLaren, 1982). Also for sugar beet, a relationship between cumulative intercepted radiation and total dry matter production was observed (Damay & Le Gouis, 1993; Hoffmann & Kluge-Severin, 2010; Martin, 1986). But this relationship could also simply be due to the increase of both parameters with time. Early leaf formation because of suitable temperatures can generally enable rapid plant development resulting in higher yields, and thus the reason is not to be attributed to the leaf alone (Werker & Jaggard, 1998). Clover et al. (2001) observed that the relationship between dry matter yield and intercepted radiation was different in stressed and virus-infected plants than in healthy, adequately irrigated plants. Also no definite relationship between leaf canopy and yield of sugar beet was observed in studies of Hoffmann (2019) and Hoffmann and Blomberg (2004), making it doubtful whether there is a reliable possibility to estimate yield based on canopy assessments. Especially under drought conditions, where leaf canopy is severely affected, it is even more difficult (Hoffmann, 2019). However, a close relationship between root diameter and root yield during most of the growing period was observed by Doney (1979) and Hoffmann (2017). It has not been tested yet whether especially under drought stress the root diameter can be used to calculate the root yield and subsequently to determine the growth rate. This would greatly contribute to a better understanding of yield formation under drought stress conditions.

The relationship between yield and water consumption is described by the water use efficiency (WUE), which indicates the amount of total dry matter or the valuable part of a crop, for example the sugar yield, which is produced with one unit of water (Boyer, 1996). Changes in growth rate and thus yield formation or changes in water consumption may lead to changes in the WUE. As a reaction to drought stress, many plants show an increasing WUE (Blum, 2009) as also observed in several field or greenhouse trials with sugar beet under drought (Barratt et al., 2021; Bloch et al., 2006; Mahmoud et al., 2018; Topak et al., 2016). For clearly delimited drought periods, no increase in WUE was observed (Brown et al., 1987). Hence, it is not clear if there is an alteration of WUE in response to drought stress and moreover if there are genotypic differences in WUE.

The objective of the study was to analyze the relationship between water use and growth of sugar beet during the season and to study the influence of drought stress on the WUE under controlled conditions in the greenhouse. Thereby, genotypic differences in water use efficiency were tested and reasons for possible differences identified.

2 Material and methods

2.1 Experimental design

Two pot experiments were conducted in the greenhouse with a growth period from March to mid of October in 2019 or mid of September in 2020, respectively (Tab. 1). Four sugar beet genotypes (hybrids) were examined which represent a range of expected drought-tolerant (genotype A and B) and susceptible (genotype C) genotypes as well as one with high sugar content (genotype D).

Pelleted, pre-germinated seeds were sown in pots (volume: 30 L, diameter: 30 cm, height: 40 cm) filled with 43 kg of sand. In order to obtain uniformly established plants, six seeds per pot were sown and thinned to one plant at 4-6 leaf stage. For the reduction of evaporation, each pot was covered with 1 kg of quartz sand (grain size: 2-4 mm). The plants received optimum nutrient supply by application of in total 3815 mg N, 2610 mg P, 6884 mg K, 2000 mg S, 590 mg Na, 1820 mg Cl, 7985 mg Ca, 1750 mg Mg and 100 mg Fe and microelements in four doses. The trials were completely randomized with five replicates per treatment and harvest date.

Optimal growth conditions were ensured by automatic control of light and temperature. The chamber was shaded when irradiance was above 50 kLux, additional light was given below 21 kLux. In March, lighting in the morning (2 hours) and in the evening (3 hours) enabled a day length of at least 12 hours. The temperature in the greenhouse was controlled by heating below 10 °C (night) or 14 °C (day). When the temperature exceeded 12 °C (night) or 17 °C (day), ventilation started. As there was no air condition, higher temperatures were reached in the greenhouse when outside temperatures were high in the summer months (Tab. 1).

Tab. 1: Climatic and trial characteristics, pot experiments in the greenhouse 2019-2020, Göttingen.

		2019		**2020**	
sowing		12.03.2019		09.03.2020	
start: ED June		1271°Cd[†]	81 dps	1281°Cd	75 dps
end: ED June/H1		1993°Cd	113 dps	1953°Cd	109 dps
start: LD Aug.		2591°Cd	142 dps	2593°Cd	141 dps
end: LD Aug./H2		3342°Cd	176 dps	3237°Cd	171 dps
H3		3999°Cd	219 dps	3672°Cd	192 dps
growth duration		219 days		192 days	
average daily temperature (°C)	March	17.0		17.5	
	April	19.5		21.5	
	May	18.6		20.1	
	June	25.6		23.7	
	July	23.7		22.9	
	August	25.4		25.1	
	September	19.9		22.1	
	October	16.9			
number of days with average daily temp. exceeding 25 °C[‡]	March	0		0	
	April	0		1	
	May	0		0	
	June	17		11	
	July	13		5	
	August	18		16	
	September	0		2	
	October	0			
	total number	48		35	

days past sowing (dps), early drought (ED), late drought (LD), harvest (H)

[†] thermal time (°Cd) as sum of daily air temperature minus a base temperature of 3°C according to Milford et al. (1985)

[‡] temperature optimum according to Kenter et al. (2006) and Terry (1968)

2.2 Water supply and drought stress treatments

Water was added on a weight basis every second day. The amount of water consumed by the plants was replenished to reach the weight of 100% (control) or 50% (drought stress) of the soil water holding capacity (WHC). The maximum WHC is the amount of water that the sandy substrate can hold and corresponds to a water tension of about pF = 1.8 (15 m%). The control treatment was sufficiently watered (100% WHC) during the whole growing period. Furthermore, there were three treatments with drought stress in different growth periods. For the duration of four weeks, drought stress was simulated either in June, in August, or drought stress in both June and August. Before and after the drought stress periods the plants were watered to 100% WHC.

2.3 Measurements and analyses

During the growth period, air temperature (°C) was recorded every hour. For the calculation of thermal time (°Cd), the average daily temperature minus a base temperature of 3°C was accumulated according to Milford et al. (1985).

The diameter of the root (cm) was measured with a caliper once a week at the widest part of the root. From the root diameter root weight was calculated using equation (1) (Hoffmann, 2017):

$$y = 90 - 60x + 12.9x^2 \qquad (1)$$

y = root weight (g FM plant^{-1})

x = root diameter (cm)

The crop growth rate (CGR) was described as the difference of dry matter between two dates and describes the increase in dry matter per unit time (Hunt, 1990, 2016). In our study, CGR was adapted to fresh matter and the growth rate was determined from the difference between the calculated root weights (fresh matter, FM) between two dates with equation (2).

$$CGR = (FM_2 - FM_1) / (t_2 - t_1) \qquad (2)$$

CGR = growth rate (g root FM d^{-1})

FM = root weight (g FM plant^{-1})

t = time (days)

The water consumption of the plants was recorded every second day as the amount of water that was needed to reach the weight corresponding to 50% and 100% of WHC, respectively. Like the CGR, the daily water consumption was determined as the amount of water consumed by a plant between two watering dates in relation to the number of days of the watering interval.

CGR and water consumption were considered in relation to thermal time. As the growth of sugar beet is controlled by thermal time (Milford et al., 1985), this allowed a joint analysis of results of both years. CGR and water consumption of the control treatment were described with log-normal functions, CGR of drought treatments with exponential functions of different orders, as those offered the best fit of the data. The order of the function was based on the number of extreme values, as physiologically described by the number of drought stress periods.

Plants were harvested after each drought stress period at the end of June or the end of August, and at the end of the growth period with 219 (2019) or 192 (2020) days after sowing, respectively (Tab. 1). Leaves were separated from the storage root below the green leaf scars.

The storage roots were washed by hand and weighted separately, and subsequently processed to a homogenous brei. One part of each brei sample was shock frozen at -70°C and stored at -26°C until analysis. The other part was dried at 105°C for 24 hours to determine the dry matter content.

The analysis of beet brei samples was carried out with an automated analyzer (Anton Paar OptoTec GmbH, Seelze) after clarification with 0.3% aluminum sulfate solution. Subsequently, sugar content in the beet brei filtrates was determined polarimetrically (ICUMSA, 1994).

The water use efficiency (WUE) was determined with equation 3 taking sugar yield as valuable part of the sugar beet crop in relation to the amount of water used (Boyer, 1996).

$$WUE = \frac{SY}{W} \tag{3}$$

SY = sugar yield (g plant^{-1}) at harvest

W = water consumption (L plant^{-1}) cumulated from sowing to harvest

2.4 Statistics

The statistical evaluation of the data set was carried out with the program SAS Version 9.4. (SAS Institute Inc., Cary, NC, USA). Data were checked for variance homogeneity and normal distribution (Kozak & Piepho, 2018). Analyses of variance (ANOVA) using SAS proc mixed with REML method and posthoc Tukey-Test ($\alpha \leq 0.05$) were carried out with the factors genotype and water supply treatment as fix, factor year as random. The SAS proc varcomp function using REML method was used for variance component analyses to estimate the contribution of year, genotype, water supply and its interaction to the overall variance. The program SigmaPlot 14.0 (Systat Software Inc.) was used to conduct regression analyses. Results are presented as bar charts with standard deviation. Significant differences were indicated with *, **, *** for error probabilities of $p \leq 0.05$, 0.01 and 0.001.

3 Results

3.1 Development of root diameter

During the season, the root diameter increased for all treatments averaged across four genotypes in both years (Fig. 1). For the control treatment a strong increase in root diameter occurred at the beginning, which slowed down as growth progressed. Under drought stress, the root diameter increased much more slowly or even decreased in the respective drought period. In the period of re-watering after drought, the root diameter increased in parallel with the control. In both years, the root diameter was highest in the control treatment and lowest in the treatment with multiple drought stress in June and August. In 2020, the root diameter was lower after early drought stress in June than after late drought stress, whereas in 2019, there was no difference. In the control, the root diameter increased from 80 to 120 mm during June 2020, and to 110 mm during June 2019.

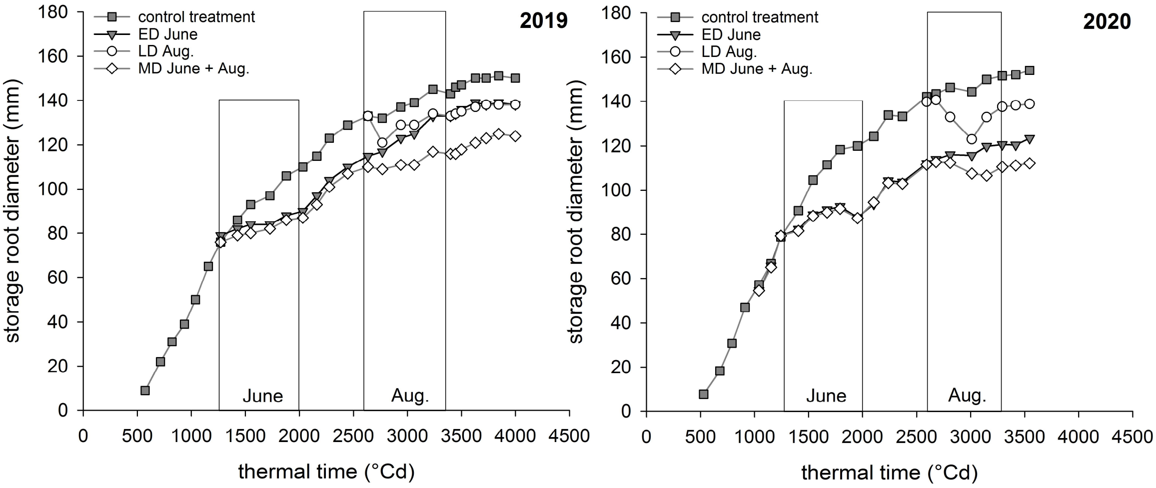

Fig. 1: Development of measured storage root diameter of sugar beet as affected by drought stress at different periods of the season (ED = early drought, LD = late drought, MD = multiple drought), mean of 4 genotypes, 5 replicates, pot trials in the greenhouse 2019 and 2020, drought stress = four weeks reduction of water supply to 50% of soil water holding capacity (WHC), control = 100% WHC, growth 219 or 192 days.

3.2 Determination of root weight by root diameter

The three harvest dates (H1-3) allow the comparison of the root weight calculated from the root diameter at harvest and the measured root weight. The deviation of the two was smaller in 2020 than in 2019 (Tab. 2). The highest deviations were 10% and 9%, which occurred for the control treatment in H2 and H3 in 2019, and in 2020 for the treatment with late drought stress in August (6%). At H3 in 2019, it is remarkable that for all treatments the calculated root weight was lower than the measured root weight.

Tab. 2: Root weight of sugar beet measured at three harvest dates (H1-3) and calculated from root diameter, mean of 4 genotypes, 5 replicates, pot trials in the greenhouse 2019 and 2020, drought stress = four weeks reduction of water supply to 50% of water water holding capacity (WHC), control = 100% WHC, growth 219 or 192 days.

harvest	**drought treatment**	**root weight at harvest** (g root FM plant^{-1})		**root weight calculated via diameter** (g root FM plant^{-1})		**relative calculated weight** (weight at harvest = 100%)	
		2019	**2020**	**2019**	**2020**	**2019**	**2020**
H 1 end of June	control	1058	1207	1000	1226	95%	102%
	June	561	550	590	552	105%	100%
	Aug.						
	June+Aug.						
H 2 end of Aug.	control	2094	2039	1879	2089	90%	102%
	June	1486	1238	1563	1234	105%	100%
	Aug.	1515	1530	1584	1586	105%	104%
	June+Aug.	1125	909	1119	916	99%	101%
H 3 Sept./Oct.	control	2309	2210	2099	2225	91%	101%
	June	1827	1326	1732	1317	95%	99%
	Aug.	1774	1852	1711	1742	96%	94%
	June+Aug.	1425	1074	1341	1040	94%	97%

3.3 Growth rate, water consumption and sugar yield

The root growth rate of the control treatment and the daily water consumption in relation to the thermal time were described best with log-normal functions (Fig. 2). From 750°Cd onwards, the growth rate increased to maximum 23 g FM plant^{-1} d^{-1} at 1750 °Cd. After that, it decreased until 4000°Cd. In parallel to the growth rate, the daily water consumption increased to a maximum of 0.9 L plant^{-1} d^{-1} and subsequently decreased. In the second part of the growth period from 2000°Cd onwards, there was a greater divergence between growth rate and water consumption than in the first part.

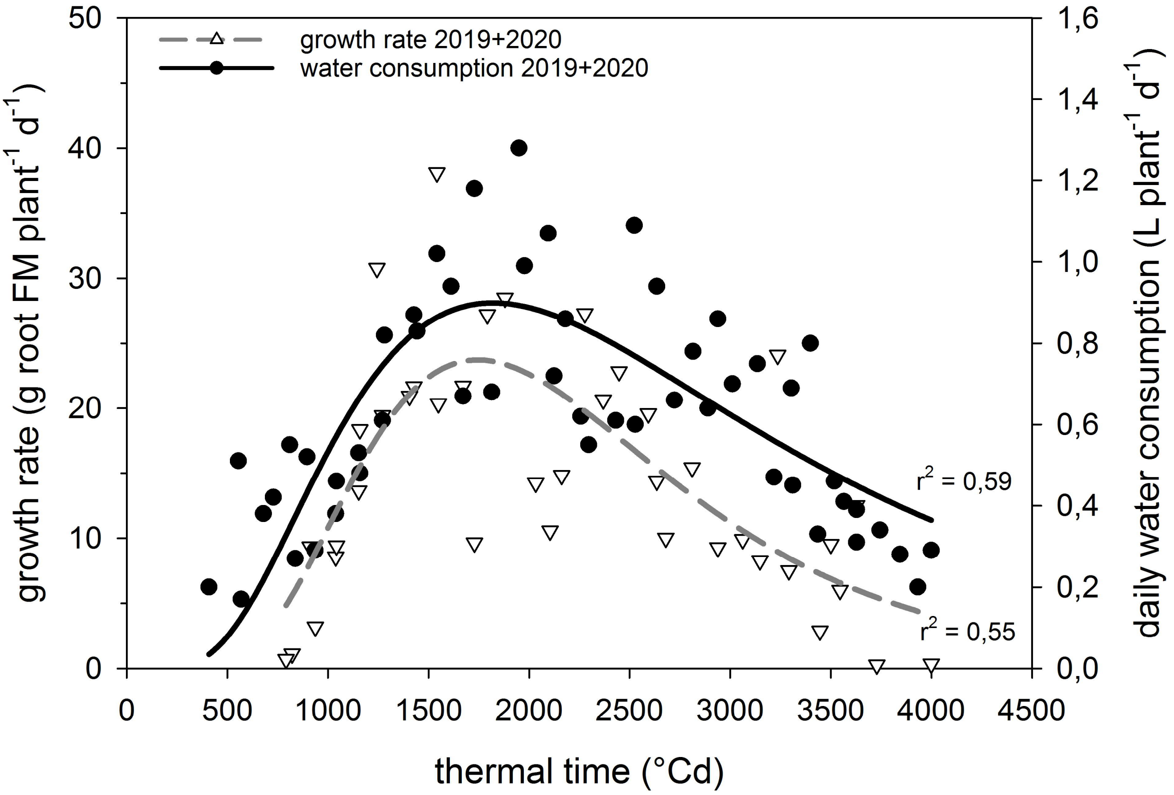

Fig. 2: Growth rate of the storage root calculated from the storage root diameter of sugar beet and measured daily water consumption at sufficient supply as related to thermal time, mean of 4 genotypes, 5 replicates, pot trials in the greenhouse 2019 and 2020, growth 219 or 192 days.

For all treatments with drought stress, the growth rates were the same as in the control treatment before the onset of drought stress (Fig. 3a-c). During the respective drought periods, the growth rates were considerably lower than those of the control treatment. After the drought period, the growth rates were close to, but not higher than those of the control treatment. Only in the end at about 3500°Cd, the drought treatments achieved partially slightly higher growth rates than the control treatment.

During the late drought period, a high variation of growth rates in the range of -55 to 55 g plant^{-1} d^{-1} was observed. However, on average, these growth rates were still distinctly lower than in the control treatment.

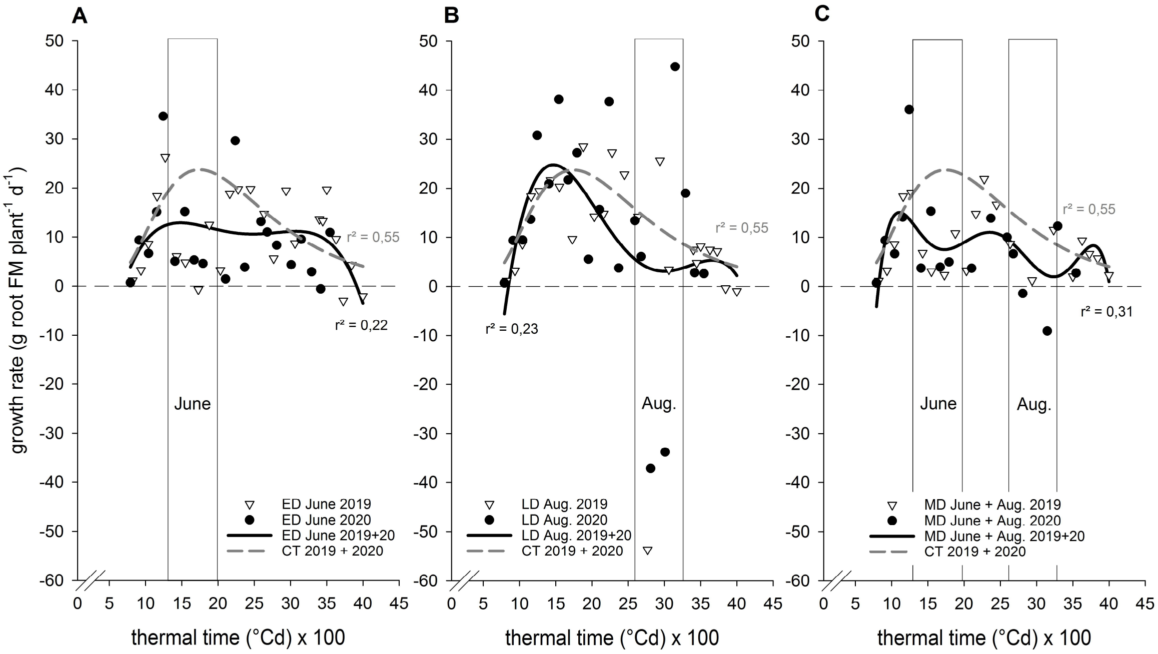

Fig. 3: Growth rate of sugar beet calculated from the storage root diameter (A) under early drought in June (EDJ), (B) under late drought in August (LDA) and (C) under multiple drought in June and August (MD June + Aug.) as related to thermal time; mean of 4 genotypes, 5 replicates, pot trials in the greenhouse 2019 and 2020, CT: control treatment with sufficient water supply, drought stress = four weeks reduction of water supply to 50% of soil water holding capacity (WHC), control = 100% WHC, growth 219 or 192 days.

The overall water consumption was higher in 2019 compared to 2020 (Fig. 4). Significant differences between treatments occurred in both years. On average of all genotypes, water consumption was highest in the control treatment and lowest in the treatment with drought stress in June and August. No significant differences between the treatments with early drought in June and late drought in August were observed in 2019. Whereas in 2020, the water consumption was significantly lower under early drought compared to late drought.

According to Fig. 2, in both years water consumption was highest in the control treatment in June and declined already in July and August. In the treatments with drought stress, water consumption was reduced in the respective months. Despite re-watering in the following months after drought, water consumption remained lower than in the control treatment.

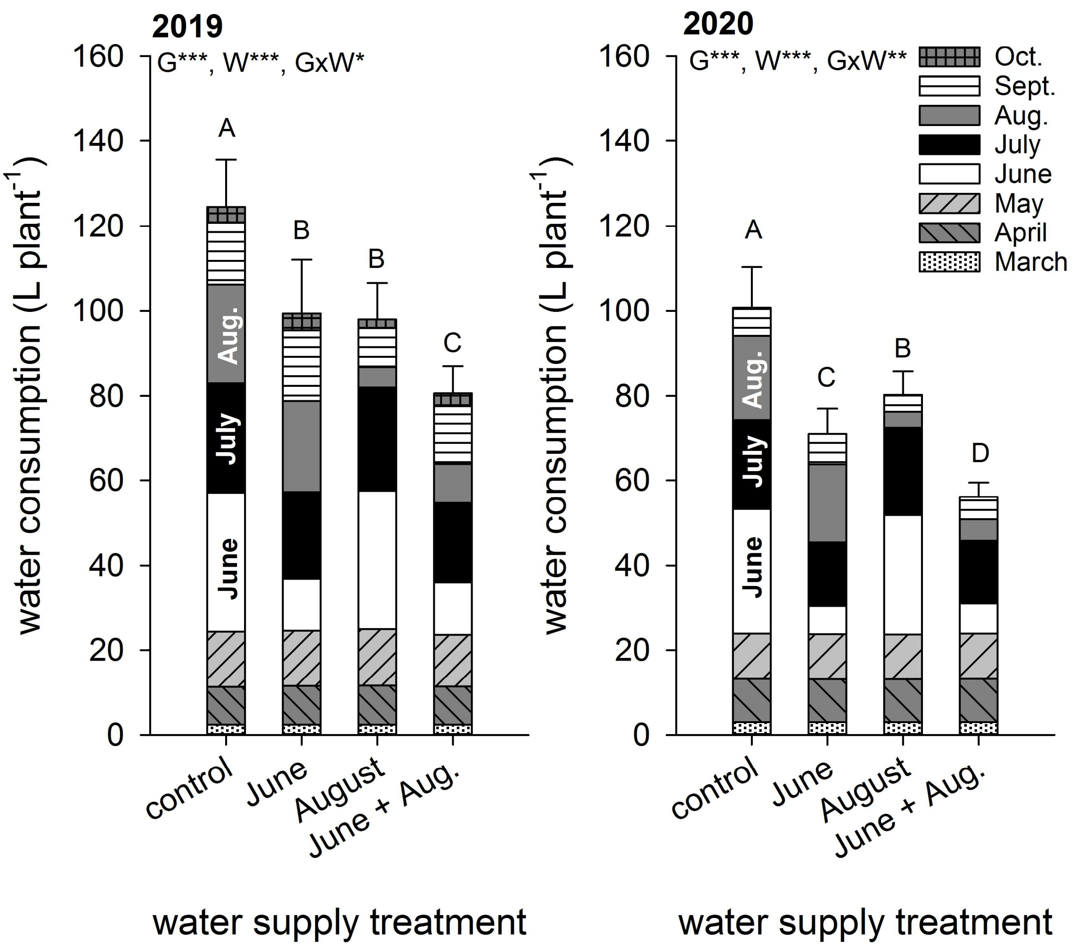

Fig. 4: Water consumption of sugar beet during the growing period as affected by drought stress in June, August or June and August; drought stress = four weeks reduction of water supply (W) to 50% of soil water holding capacity (WHC) in the respective month, control = 100% WHC, mean of 4 genotypes (G), 5 replicates, pot trials in the greenhouse 2019 and 2020, growth 219 or 192 days, *, **, *** significant at $P < 0.05$, $P < 0,01$ and $P < 0.001$, different letters indicate significant differences between water supply treatments averaged across four genotypes, $\alpha = 0.05$ (Tukey-test).

Genotypic water consumption differed significantly from 95 to 111 L plant $^{-1}$ (2019) and 75 to 85 L plant $^{-1}$ (2020) on average of all water supply treatments (Fig. 5 top). In both years, genotype D had the significantly highest water consumption, while genotype A, B, and C did not significantly differ in water consumption (around 97.0 (2019) or 75.6 L plant^{-1} (2020)). An interaction between genotype and drought treatment occurred in both years, but the contribution to the total variance was only 3.2% and 1.9% (Tab. 3).

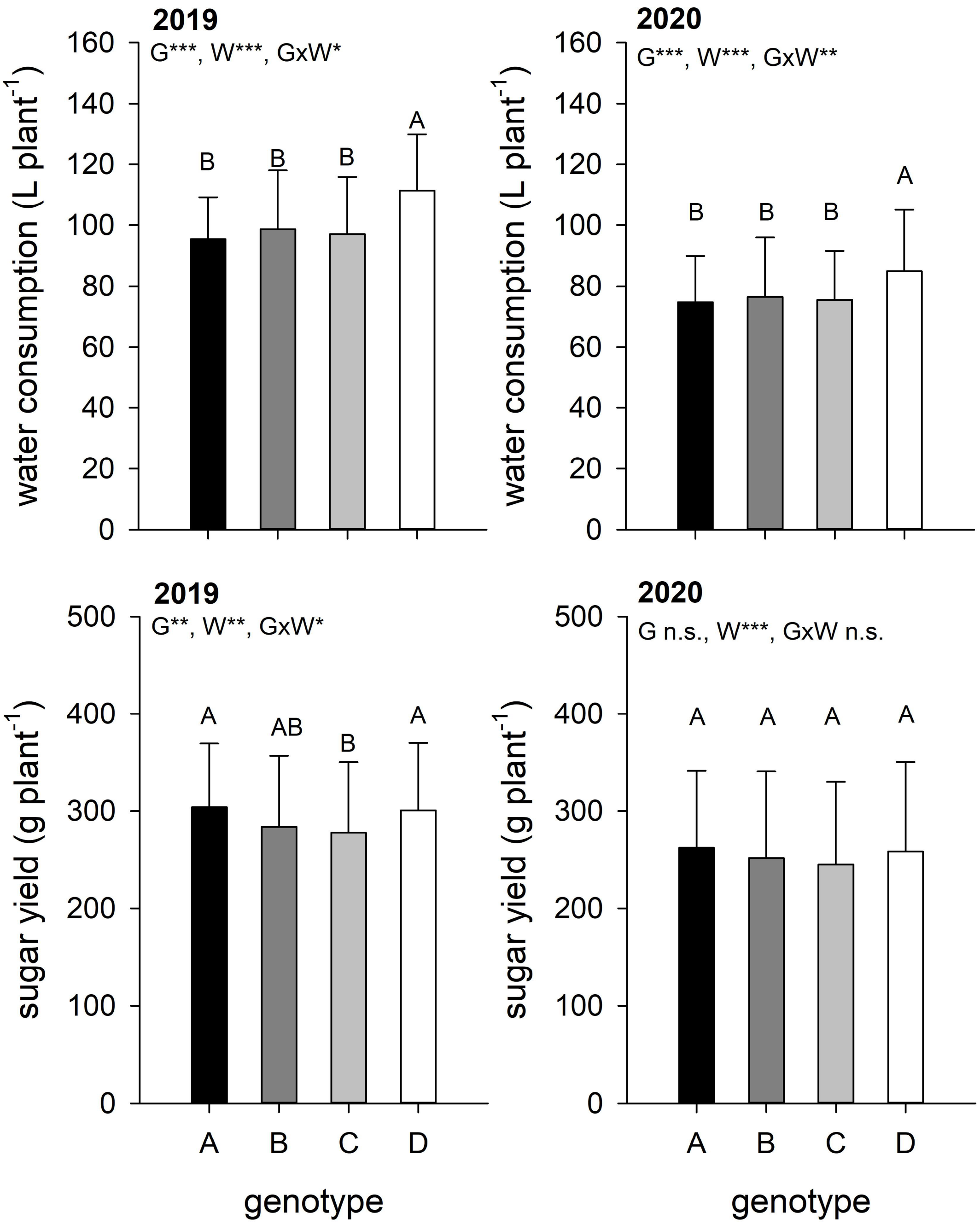

Fig. 5: Water consumption (top) and sugar yield (bottom) of sugar beet genotypes (G), mean of 4 water supply treatments (W), 5 replicates, pot trials in the greenhouse 2019 and 2020, drought stress = four weeks reduction of water supply to 50% of soil water holding capacity (WHC), control = 100% WHC, growth 219 or 192 days, *, **, *** significant at $P < 0.05$, $P < 0,01$ and $P < 0.001$, different letters indicate significant differences for genotypic water consumption averaged across four water supply treatments, $\alpha = 0.05$ (Tukey-test).

Tab. 3: Variance components of water consumption, sugar yield and water use efficiency (WUE) of sugar beet, pot trials in the greenhouse 2019 and 2020, 4 genotypes, 5 replicates, three harvest dates (H), drought stress = four weeks reduction of water supply (W) to 50% of soil water holding capacity (WHC), control = 100% WHC, growth 219 or 192 days.

		% of total variance								
		year (Y)	genotype (G)	water supply (W)	YxG	YxW	GxW	YxGxW	repl.	error
water consumption	2019	-	10.8	74.0	-	-	3.2	-	0.5	11.4
	2020		4.7	88.5			1.9		0.1	4.8
sugar yield	2019	-	1.2	83.2	-	-	3.7	-	0.5	11.5
	2020		0	90.3			0.9		1.8	7.0
WUE	H1	62.7	12.7	0	1.2	3.6	3.4	0	3.8	12.7
WUE	H2	16.1	20.5	16.3	3.1	25.7	0.1	0	2.8	15.4
WUE	H3	11.8	15.3	6.2	0	46.5	2.8	0	0.6	16.8

The sugar yield amounted to 292 (2019) and 255 g sugar plant^{-1} (2020) averaged over water supply treatments and genotypes at final harvest (Fig. 5 bottom). In 2019, there were small, but significant differences between the genotypes, whereas no significant genotypic differences and no genotype by water supply interaction occurred in 2020. In both years, greatest contribution to the overall variance came from water supply (Tab. 3). The contribution of genotype, as well as of the genotype by water supply interaction was below 4%.

3.4 Water use efficiency (WUE)

The WUE varied among the genotypes from 2.5 to 3.5 g sugar L^{-1} on average of all water supply treatments across all harvest dates (Fig. 6). Genotype A had the significantly highest WUE, genotype D the significantly lowest WUE for all harvest dates. Genotypes B and C were intermediate. At harvest H2, no interaction between genotype and drought treatment occurred, whereas at harvest H1 and H3 a significant G by W interaction occurred. The contribution of the interaction to the total variance was below 3.5% for all harvest dates (Tab. 3).

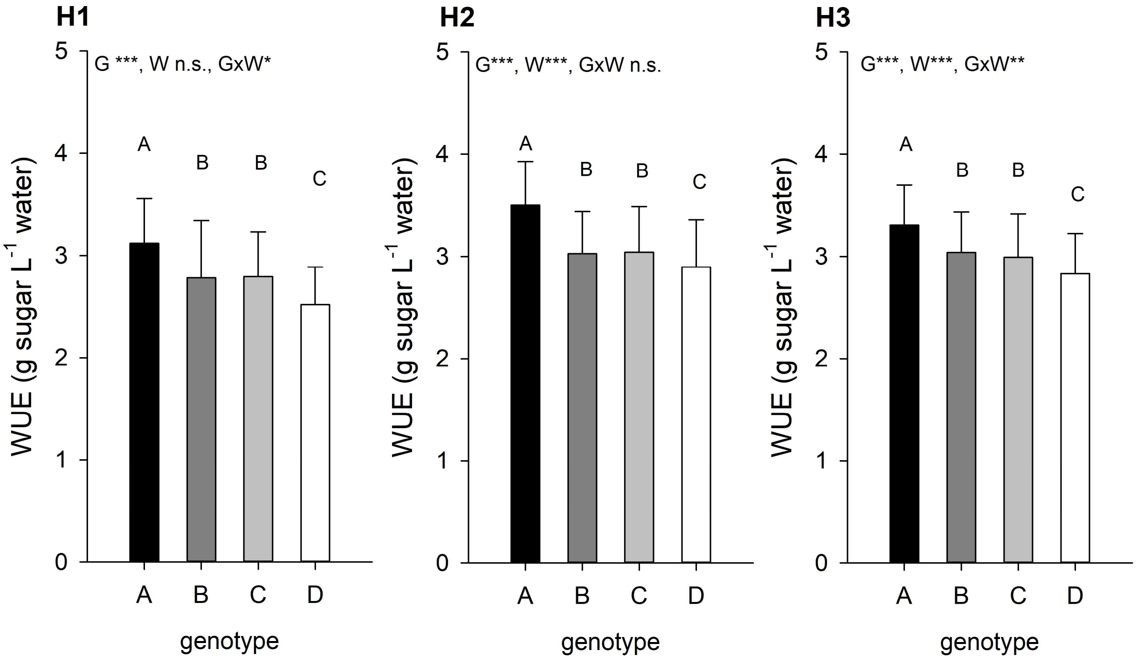

Fig. 6: Water use efficiency (WUE) of four sugar beet genotypes (G) harvested end of June (H1), end of August (H2) and September/October (H3), mean of four water supply treatments (W) with different drought periods, drought stress = four weeks reduction of water supply to 50% of soil water holding capacity (WHC), control = 100% WHC, 5 replicates, pot trials in the greenhouse 2019 and 2020, growth 219 or 192 days, *, *** significant at $P < 0.05$ and $P < 0.001$, n.s. = not significant, different letters indicate significant differences for genotypic WUE averaged across four water supply treatments, $\alpha = 0.05$ (Tukey-test).

4 Discussion

Pot trials in the greenhouse allow the exact simulation of drought stress in defined growing periods. Confounding factors such as pests and diseases can be excluded, so that the effect of drought on yield formation and water use of sugar beet genotypes can be investigated specifically and with high precision.

In contrast to field trials, pot experiments allow the determination of yield and water consumption of individual plants. However, fibrous root growth is restricted by the pots. Under drought stress conditions in the field, fibrous root growth can exploit water resources in deeper soil layers (Morillo-Velarde & Ober, 2006; Scott & Jaggard, 1993). However, Fitters et al. (2017; 2018) observed a duration of up to 16 days for new roots to exploit water resources in deeper soil layers. During this time, yield restrictions due to drought should have already occurred, so that drought stress cannot be completely avoided by a deeper root system (Hoffmann et al., 2020). Therefore, in this greenhouse experiment, the effect of drought stress on sugar beet growth was studied independently of the influence of the root system.

4.1 Description of sugar beet growth with the root diameter

In order to determine in which period the growth and thus the demand for resources is the highest, the growth process needs to be described. Sugar beet growth can be described non-destructively without successive harvests with the root diameter, as this parameter is closely related to the root weight (Doney, 1979; Hoffmann, 2017). In the greenhouse trials of the current study, the control treatment ended up with the highest root diameter in both years. In 2020, the treatment with early drought in June had a lower diameter than the treatment with late drought in August. This is supported by the measured sugar yield data. Therefore, it can be concluded that early drought had a stronger impact on yield formation than late drought, which confirms previous observations by Brown et al. (1987).

In 2019, there was a partial deviating response showing no differences in root diameter between early drought in June and late drought in August. As more days with temperatures above 25°C occurred in 2019 compared to 2020, the optimal temperature range of 17-25°C for sugar beet growth was exceeded (Kenter et al., 2006; Terry, 1968), because the greenhouse was not air-conditioned. This points to growth restrictions due to heat stress. Despite unlimited water supply, the growth of the control and the late drought treatment might thus have been restricted by heat stress in June and in July, too, also evident from the lower final root diameter compared to 2020.

The root diameter was used in the current study to estimate root weight and to calculate the growth rate. The calculated weight was compared with the measured weight at the three harvest dates. They deviated by less than 5% for most treatments and harvests. A lower calculated root weight at the final harvest can probably be explained by a greater increase in aboveground growth in later stages, which cannot be determined by an increase in root diameter (Hoffmann et al., 2020).

Because of this minor deviation, it can be assumed that the growth rate calculated with the root diameter adequately reflect the growth. In the current study, under sufficient water supply, there was a strong increase in growth rate in the beginning. The maximum growth rate was reached at a thermal time of approximately 1750°Cd. This maximum growth rate is in a similar order as found by Hoffmann et al. (2020) (18 g root dry matter (DM) m^{-2} d^{-1}) and Bloch and Hoffmann (2005) (15 g root DM m^{-2} d^{-1}) in field trials. Lower growth rates in field trials compared to the pot experiments can be explained with a higher plant population resulting in limited access to resources such as light, space and water due to inter-plant competition (Jaggard & Qi, 2006). In addition, a higher yield potential due to breeding progress in the past 15 years and thus higher growth rates can also be assumed for the current study.

The growth rate peaked at a thermal time of 1750°Cd, corresponding to 105 (2019) or 103 (2020) days after sowing, similar to evaluations by Hoffmann et al. (2020) with 1600°Cd (140 days after sowing, end of August). In the greenhouse, the peak was reached earlier than in the field in terms of number of days or day of the year compared to field conditions because of optimal temperature and light conditions, especially during emergence and early development. Obviously, in the period with the highest growth rate (in the greenhouse: June) a restriction due to drought stress has the greatest impact on yield formation. Therefore, it can be concluded that the effect of drought stress is stronger at the beginning of the season than at the end.

4.2 Relationship between growth and water consumption

In the current study, measured water consumption and calculated growth rate developed simultaneously in the sufficiently watered control treatment. After their parallel increase up to the maximum, this relationship became marginally less close in the second half, probably caused by unproductive water loss due to evaporation because of high temperatures in summer.

In crop growth models it is often considered that, in the absence of diseases, sugar beet growth is either limited by radiation or water supply (Baey et al., 2014; Qi et al., 2005). But this view changes gradually. Although in older literature the relationship between sugar beet growth and water use was attributed to the control by stomatal conductance (Scott & Jaggard, 1993), more recent studies point to additional factors (Bloch et al., 2006; Monti et al., 2005; Wedeking et al., 2018). There is some evidence that the photosynthetic activity in leaves, i.e. the source for assimilates, is limited by the demand in the sink (Paul & Foyer, 2001). Today it is widely accepted that the growth rate of a crop controls the photosynthetic activity and thus the demand for resources such as water (Fatichi et al., 2014; Körner, 2013, 2015; White et al., 2016).

The view that the water demand is controlled by the sink and thus by the growth rates is emphasized by the finding that for the control treatment the water consumption was always closely related to the growth rate and declined in later growth phases, despite unlimited water availability. The reduction in growth rate may be caused by the decline in day length later in the season, so that intercepted radiation may be reduced as a result of photoperiodism

(Adams & Langton, 2005; McMaster & Moragues, 2018). However, this effect is expected to have only a minor influence in our experimental set-up, as long-day conditions were ensured by additional lighting in the greenhouse at the beginning and end of the season. Furthermore, in a pot experiment with sugar beet Schnepel and Hoffmann (2016) found a comparable growth even when the plants were sown at different times of the year suggesting a general growth pattern with a decline of growth rates (and thus water demand) after the maximum.

In the drought stress treatment, even direct re-watering after drought stress did not lead to a direct recovery of growth and water consumption. Despite potentially unlimited water supply, the water consumption in the month after drought stress was still lower compared to the unstressed control. This may indicate a lower water demand due to restricted growth.

There is much evidence that sugar beet is in most growth stages sink, not source limited (Hoffmann, 2019; Hoffmann et al., 2020), and therefore the assimilate supply is probably not the limiting factor (Hoffmann, 2010). At the onset of a drought period, the sink and therefore the activity in storing assimilates is limited (Körner, 2013). The reason is that cell expansion in the storage root as a sink is the most drought-sensitive metabolic process, much more than photosynthesis or sugar accumulation (Hsiao, 1973). When assimilates cannot be stored in the root, they accumulate in leaves and, as a result, photosynthetic activity and thus water demand are downregulated (Körner, 2013; Paul & Foyer, 2001). Therefore, drought in a period with high growth rates and correspondingly high water demand will cause greater growth and yield restrictions than in a growth period with lower growth rate and thus lower water demand.

4.3 Reasons for genotypic differences in WUE

The WUE combines yield in relation to water consumption (Boyer, 1996). The average WUE of the genotypes in the greenhouse of about 3 g sugar L^{-1} was within or slightly above the range reported from field trials by Brown et al. (1987), Dunham (1993) and Rinaldi and Vonella (2006). The slightly higher WUE in this greenhouse trial can be explained with a higher yield of individual plants compared to a plant population with intercrop competition under field conditions.

In the current study, no relevant differences in sugar yield between the genotypes were detected. Conversely, genotypic differences in water consumption occurred, which caused the genotypic differences in WUE. The differences in water consumption can be explained with theoretically unlimited water supply in the greenhouse, as every second day the consumed water was replenished to 50% or 100% of WHC, respectively. Under field conditions, however, the situation is opposite: water supply is limited and is the same for all genotypes. Therefore, when the WUE differs, genotypic differences in yield will occur.

This was recently demonstrated with the same genotypes in multi-environmental field trials where water supply was limited even for an extended period (Ebmeyer et al., 2021). In these field trials comparing plots with and without irrigation, the genotype ranking for sugar yield was consistent with that for WUE in the current greenhouse trials. Although Ober and Luterbacher (2002) found genotype by irrigation treatment interactions in prebreeding material, the negligible genotype by environment interaction (in the absence of pest and diseases) is in accordance with former studies with sugar beet hybrids (Bloch & Hoffmann, 2005; Hoffmann et al., 2009; Ober et al., 2004). This confirms that genotypic differences arose independently of the environment and thus water supply.

In the greenhouse trials of the current study, the genotype by water supply interaction was also only minor. This underlines the view that genotypic differences in WUE arise mainly from genotypic differences in yield potential which seems to be the driving factor for the demand on water supply. Therefore, breeding should focus on yield potential in the development of varieties adapted for environments with varying water supply. Nevertheless, it would be interesting to compare the WUE in the greenhouse in response to extended drought periods with WUE in limited drought periods of the current study.

5 Conclusions

Our study emphasizes that the growth rate of sugar beet determines the water demand. Consequently, the period with the highest growth rate in early summer is also the period with the highest sensitivity to water shortage.

No relevant interaction between sugar beet genotype and water supply was observed for WUE. Under natural conditions in the field, genotypes with a higher WUE can produce higher yields with the available water, regardless of drought stress. The results of the current study suggest that for sugar beet, genotypic differences in WUE are the consequence of genotypic differences in sugar yield potential. Therefore, for the development of sugar beet varieties with adaption to drought stress conditions, a high sugar yield potential should be considered as the main trait for selection as well.

Investigations by Hoffmann (2019) point to genotypic differences in assimilate partitioning as an important cause for genotypic differences in sugar yield. It remains to be investigated whether the genotypic proportion of leaf mass and thus assimilate partitioning plays a role for the WUE. The genotypic proportion of leaf mass could be an interesting factor determining nitrogen use efficiency (NUE) as well, which relates yield and nitrogen supply. However, it is not known whether NUE, like WUE, is also substantially determined by sugar yield potential. Further research is needed to investigate this issue.

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Manuskript II

Drought tolerance of sugar beet - evaluation of genotypic differences in yield potential and yield stability under varying environmental conditions[2]

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Abstract

Drought stress affects yield formation of sugar beet. Under climatic changes with longer periods of drought, the development of sugar beet varieties with a higher drought stress tolerance is gaining importance. Objectives of the study were to investigate genotypic differences in the response to different environments, especially drought stress, to define conditions in which sugar beet can best be selected for root yield and sugar content, and furthermore, to examine the relation between yield potential and yield stability. In 2018 and 2019, field trials were carried out with 6 genotypes at three drought-stressed sites, where an irrigation treatment allowed the comparison with optimal growth conditions, furthermore, trials with 3 N treatments were conducted. In the absence of diseases, no significantly different regression slopes of genotypes were observed for sugar yield in 17 environments. Hence, the trials provided no indication for a special adaptation of the genotypes to drought stress conditions. One reason might be a sink limitation of sugar beet growth. By contrast, a genotype by environment interaction existed for sugar content and root yield. The greatest genotypic discrimination to classify genotypes with either high root yield or sugar content was under optimal growing conditions. With increasing root yield, the sugar content declined similarly in all genotypes. For sugar yield, differences between the genotypes occurred in yield potential and yield stability. High yield potential was not necessarily associated with high yield stability. As it is important to achieve consistently high yields also with higher variability of climatic conditions, yield stability will increase in importance for future breeding.

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Keywords

genotype, environment, interaction, nitrogen supply, drought stress, water supply

1 Introduction

The impacts of climatic changes are expected to reduce the frequency and intensity of summer precipitation (IPCC, 2013). Periods of drought in the summer months are the consequence. For sugar beet, limited water availability constraints yield formation and leads to poorer processing quality (Bloch et al., 2006; Bloch and Hoffmann, 2005; Ebmeyer and Hoffmann, 2020; Ober and Luterbacher, 2002). Therefore, adapted varieties that can cope with such challenging environmental conditions are needed.

Adaptions to different environmental conditions such as drought are known for cereals (Ceccarelli, 1994; Denčić et al., 2000). These adaptions are the result of interactions between genotype and environment (Chloupek and Hrstkova, 2005), which were observed in experiments in different European countries (Annicchiarico, 2002; Patterson et al., 1977; Weber and Westermann, 1994). When such interactions occur, the genotype differences vary between the environments and in case of extreme variation of these differences, the genotype ranking can change under different environmental conditions. Genotypes with a high rank only in environments with drought are specially adapted to these unfavorable growth conditions, but consequently not to other more favorable environmental conditions. As the performance is not consistent across different environments, a large number of test environments is necessary for the development of the respective adapted varieties. From the breeder’s perspective, an ideal variety would be tested in a limited number of environments, but would perform well in a wide range of different environments. Such genotypes with a wide adaption keep their ranking across different environments due to negligible or lack of interaction with the environment (Blum, 2005; Ceccarelli, 1994).

For sugar beet, it is still under discussion, whether varieties with special adaptions to drought exist, or quite the contrary, whether sugar beet is broadly adapted to different environmental conditions. Sugar beet field trials in 52 different environments across Europe pointed to a wide adaption as for sugar yield only a negligible GxE interaction occurred (Hoffmann et al., 2009). However, the genotypes were chosen according to their quality characteristics, not to putative drought tolerance. Moreover, there was no direct comparison of limited and adequate water supply at the same site. The effect of drought was examined by Ober et al.

(2004) under a polythene tunnel to exclude other factors. The results suggest stable yields and in particular, a similar variety ranking under both drought stress and sufficient water supply. However, these results were obtained under more artificial conditions at only one site. Whether the response of sugar beet genotypes to drought stress under field conditions is similar in a broad range of environments is not yet clear. This information is essential to assess the necessity for the development of drought tolerant varieties, and furthermore, for the identification of the most discriminating environments for variety selection.

An ideal genotype would combine high yield potential with yield stability (Ober and Luterbacher, 2002). The yield potential is defined as the yield, which can theoretically be achieved without limitations by pests, diseases or restrictions in water or nutrient supply or other environmental factors (Evans and Fischer, 1999). Environmental yield stability is derived from the Shukla variance and describes to which extent a genotype deviate from the expected response in the respective environment. In each of different environments, a stable genotype has no deviation from the expected response and performs completely to the estimated level (Becker and Léon, 1988). A genotype can still be superior even with a slightly lower yield potential, but if instead the stability is high, so that the yield corresponds completely to the estimated level (Kang, 1993). However, for sugar beet it is not known whether high yielding genotypes also provide a high yield stability in changing environments.

The objectives of the present study were (1) to quantify the yield response of sugar beet genotypes in different environments, in particular under drought stress conditions, (2) to determine environments suitable for the selection of genotypes, and (3) to analyze the relation between yield potential and yield stability.

2 Material and Methods

2.1 Field trials

In 2018 and 2019, six sugar beet genotypes were cultivated in field trials at Monselice (Italy), Orleans (France), Leeheim (Germany) and Göttingen (Germany) (Tab. 1). The six genotypes were chosen to represent a range of drought-tolerant (genotype 1 and 2) and susceptible (genotype 3) genotypes as well as different yield-types with either high sugar content (genotype 5), high root yield (genotype 4) or high marc content (genotype 6). All genotypes were hybrids and tolerant to rhizomania.

Water availability or nitrogen supply were varied at different sites (Tab. 1). At the sites Monselice, Orleans and Leeheim, plots with full irrigation and without irrigation were established. In the non-irrigated treatments, drought stress was achieved, as the sites are characterised by low precipitation and high temperature. In the irrigated plots, sufficient water was supplied for optimal sugar beet growth by an irrigation boom with special nozzles, which ensured optimal water distribution while avoiding wind drift. At each site, two identical, but separate field trials with the same randomized block design in four replications were established next to each other. The difference was that one received the irrigation treatment, the other one was rainfed. A safe distance between both trials avoided neighbouring effects. These pairs of trials were conducted at the different sites in the two different years and hence could be regarded as replication for the irrigation treatment according to Piepho et al. (2016). Plots consisted of three rows with 8 m length (10.8 m^2).

In 2018, the non-irrigated plots at Leeheim could not be harvested due to severe infestation with beet moth. Furthermore, drought stress did not occur after high rainfall at Monselice in 2018. Therefore, these sites had to be discarded for the statistical evaluation of the effect of irrigation. In the statistical evaluation of yield stability, however, the irrigated treatment of Leeheim 2018 and both the irrigated and non-irrigated treatment of Monselice 2018 were included as single environments.

At Göttingen, different amounts of nitrogen fertilizer were tested under rainfed conditions. Calcium ammonium nitrate was added to reach 60, 120 and 240 kg N ha^{-1}, including the soil mineral N content before sowing in 0-90 cm (approx. 60 kg N ha^{-1} in both years). N fertilizer was applied by hand, and the highest treatment (240 kg N ha^{-1}) was split into two doses (after sowing, at 4 to 6 leaves stage) to avoid salt stress. Genotypes and N treatments were completely randomized in a two factorial block design with four replicates. Plots included nine rows of 8 m length, of which rows 2, 3, 4 were harvested in October. The outer rows served as border, while rows 6, 7, 8 were used for a harvest in August.

Due to different conditions regarding soil texture, temperature and precipitation, sowing and harvest dates differed among environments, so that the duration of the growing period varied from 139 to 175 days (Tab. 1). All trials had a plant population of about 90.000 plants ha^{-1}. Plant protection measures were carried out according to the regional guidelines of good agricultural practice to control weeds, pests and diseases.

Tab. 1: Site characteristics of the field trials in 2018 and 2019.

Year	Country	Site	Treatment	Soil type	Mean temperature during growth (°C)	Thermal time (°Cd)[a]	Precipitation (mm)	Irrigation (mm)	Growing period (d)
2018	Italy	Monselice	irrigated	Silt loam	17.0	1979	344	160	141
			non-irrigated		17.1	1970	344	0	140
2018	France	Orleans	irrigated	Loam	18.0	2497	359	160	166
			non-irrigated		18.1	2468	359	0	162
2018	Germany	Leeheim	irrigated	Sandy clay loam	17.5	2201	232	395	151
			non-irrigated		------ severe infestation with beet moth, no harvest possible ------				
2019	Italy	Monselice	irrigated	Silt loam	19.3	2751	401	160	169
			non-irrigated		19.3	2730	401	0	168
2019	France	Orleans	irrigated	Loam	17.1	2442	189	190	173
			non-irrigated		17.2	2421	189	0	171
2019	Germany	Leeheim	irrigated	Sandy clay loam	18.7	2771	406	120	175
			non-irrigated		18.8	2577	406	0	162
2018	Germany	Goettingen	0 kg N ha^{-1}	Silt loam	17.5	3064	219	0	175
			120 kg N ha^{-1}						
			240 kg N ha^{-1}						
2019	Germany	Goettingen	0 kg N ha^{-1}	Silt loam	15.3	2807	350	0	183
			120 kg N ha^{-1}						
			240 kg N ha^{-1}						

[a] thermal time as sum of daily air temperature minus a base temperature of 3 °C according to Milford et al. (1985)

2.2 Harvest and sample analysis

In autumn, the crops were machine harvested at Monselice, Orleans and Leeheim and manually topped and lifted at Göttingen. After transport to the tarehouse, the storage roots were washed, weighed to determine the root yield and processed to a homogenous beet brei. Brei samples were shock frozen at -40 °C and stored at -20 °C until analysis.

In a central quality laboratory, beet brei samples were analyzed with an automated analyzer after clarification with 0.3% aluminium-sulphate solution. Subsequently, the sugar content in the beet brei filtrates was determined polarimetrically (ICUMSA, 1994).

Sugar yield was calculated from root yield and sugar content of the beets.

2.3 Statistics

The statistical analysis of the data set was conducted with the program SAS Version 9.4 (SAS Institute Inc., Cary, NC, USA). Data were analysed in two steps after being tested for normal distribution and variance homogeneity (Kozak and Piepho, 2018). Subsequently an analysis of variance (ANOVA) using SAS PROC MIXED procedure was carried out.

In the first step of the evaluation, the effect of drought stress on sugar yield was analysed by comparing the treatments (irrigated/non-irrigated) at four sites where considerable yield differences between irrigated and non-irrigated treatments occurred. According to Piepho et al. (2016) an evaluation with the raw data averaged over all sites for each genotype and treatment was carried out with the SAS PROC MIXED procedure using REML with the following model:

$$y_{ilst} = a_{st} + f_{lt} + G_{is} + e_{ilst}$$

where y_{ilst} is the yield of the genotype i in the block l for the stress level $s = 1$ (non-irrigated) applied to trial area $t = 1$ only and stress level $s = 2$ (irrigated) applied to trial area $t=2$ only, a is the general intercept, f_{lt} is the effect of the block l in the respective trial area t, G_{is} is the effect of the genotype i for the stress level s, e_{ilst} is the error. A Tukey-test for comparison of mean values followed. These results are presented as bar charts with standard deviation.

In the further evaluation, each treatment (irrigated/non-irrigated) at each site in each year was considered as a single environment. In addition to the eight environments with differences in water supply, three environments were added where precipitation was too high to simulate sufficient drought stress (Monselice 2018) or only the irrigated plots could be harvested due to beet moth infestation in the drought stress plots (Leeheim 2018). Furthermore, another six environments with differences in N supply were added (Göttingen 2018, 2019). In total, 17 environments with different growing conditions for sugar beet were included to analyse the genotypic yield response.

The SAS PROC MIXED procedure was carried out with the factors environment and genotype. The environments are the combination of different treatments at different sites in different years and were therefore regarded as random. The factor genotype was regarded as fix because the six genotypes were chosen with regard to differences in their response to drought (Annicchiarico, 2002).

For analysis of the genotype by environment interaction, a joint regression analysis according to Eberhard and Russel (1966) as an extension of the regression by Finlay and Wilkinson (1963) was carried out. Thereby, the effect of genotype i in the environment j (GE_{ij}) was regressed on means of environments (Becker and Léon, 1988).

This was modelled in SAS using REML with the function:

$$GE_{ij} = b_iE_j + d_{ij} = a_j + b_im_j + d_{ij}$$

where b_i is the regression coefficient for the genotype *i*, E_j is the environment main effect, d_{ij} is the deviation from the model as RMSE (for each genotype separate), the residual of the genotype x environment interaction, and in the second expression a_j is the intercept, m_j is the grand mean in environment *j* (Annicchiarico, 2002; Becker and Léon, 1988; Hoffmann et al., 2009). According to Eberhart and Russell (1966) in the dynamic concept by Becker and Léon (1988), genotypes with *b* not significantly different to 1 are defined as stable and indicate minor genotype x environment interaction (Annicchiarico, 2002). Significant effects are indicated with *, **, or *** for $p < 0.05$, 0.01, 0.001, or n.s. = not significant.

For the evaluation of yield potential and yield stability, the yield stability index (YSI) by Kang (1993) was determined. This index allows the identification of genotypes with a high yield potential in combination with high yield stability in different environments. For this purpose, the yield is ranked, and the environmental stability is determined based on Shukla's stability variance (Shukla, 1972). Lower values for the variance indicate a higher stability of the genotype. The sum of the adjusted yield ranking and the rating of the stability variance results in Kang's YSI (Kang, 1993). According to Cotes et al. (2002) an ANOVA with SAS PROC MIXED procedure was made for the mean yield comparison as prerequisite for the genotypic yield rank. Shukla's stability variance was estimated by REML and modelled in SAS with the function:

$$y_{ijk} = m + G_i + r_{jk} + E_j + (GE)_{ij} + e_{ijk}$$

where y_{ijk} is the yield of the replicate *k* of the genotype *i* in the environment *j*, *m* is a general mean, G_i is the *i*th genotype main effect, E_j is the environment *j* main effect, r_{jk} is the effect of block *k* in the environment *j*, $(GE)_{ij}$ is the *ij*th genotype-environment interaction effect and e_{ijk} is the experimental error, according to Shukla (1972) and Piepho (1999). Genotypes with YSI above the mean are determined as superior, genotypes with YSI below the mean are determined as inferior.

Shukla's stability variance and sugar yield of each individual genotype were considered relative to the mean of Shukla's stability variance or mean sugar yield of all genotypes in 8 and 17 environments, respectively. This allowed the examination of Shukla's stability variance of sugar yield in 8 as compared to 17 environments.

3 Results

The sugar yield differed significantly between the irrigated and the non-irrigated treatment averaged over four sites (Fig. 1). The average sugar yield for all genotypes under irrigation was 17.2 t ha^{-1}. Under drought stress, the sugar yield was on average about 30 % lower and reached only 12.0 t ha^{-1}, whereby the extent of drought stress and thus the yield reduction varied at the different sites (data not shown). Furthermore, there were significant differences between the genotypes, but no significant interaction between genotype and irrigation treatment.

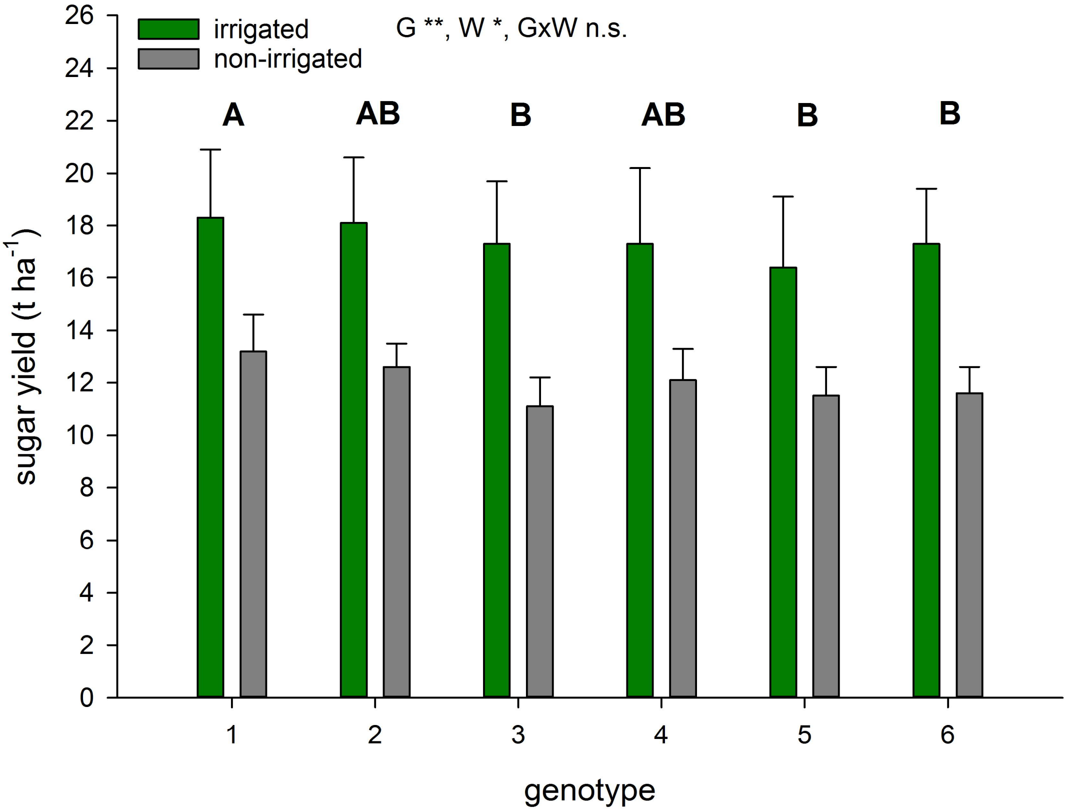


Fig.1: Sugar yield of six sugar beet genotypes (G) as affected by water supply (W: irrigated, non-irrigated = drought stress), mean of field trials in Italy 2019, France 2018, 2019 and Germany 2019, *, ** significant at $P < 0.05$ and $P < 0.01$, n.s. = not significant, same letters indicate no significant differences for mean sugar yield averaged for both treatments between genotypes, $\alpha = 0.05$ (Tukey-test).

In a further step, the two irrigation treatments at the chosen sites were regarded as eight individual environments with differences in water supply (sufficiently watered or drought stressed). This allowed the comparison of the sugar yield of a single genotype in relation to the mean of all genotypes in the given environment (Fig. 2). The sugar yield in the environments ranged from 11.3 t ha^{-1} under unfavourable conditions to 19.7 t ha^{-1} under more favourable conditions. Within the environments, the genotypes differed significantly in sugar yield. There was a significant interaction between genotype and environment. However, for all genotypes, the slope of the regression line was not significantly different to 1. Nevertheless, genotype 3 with the highest slope (1.05) showed a tendency for higher sugar yields under favourable conditions.

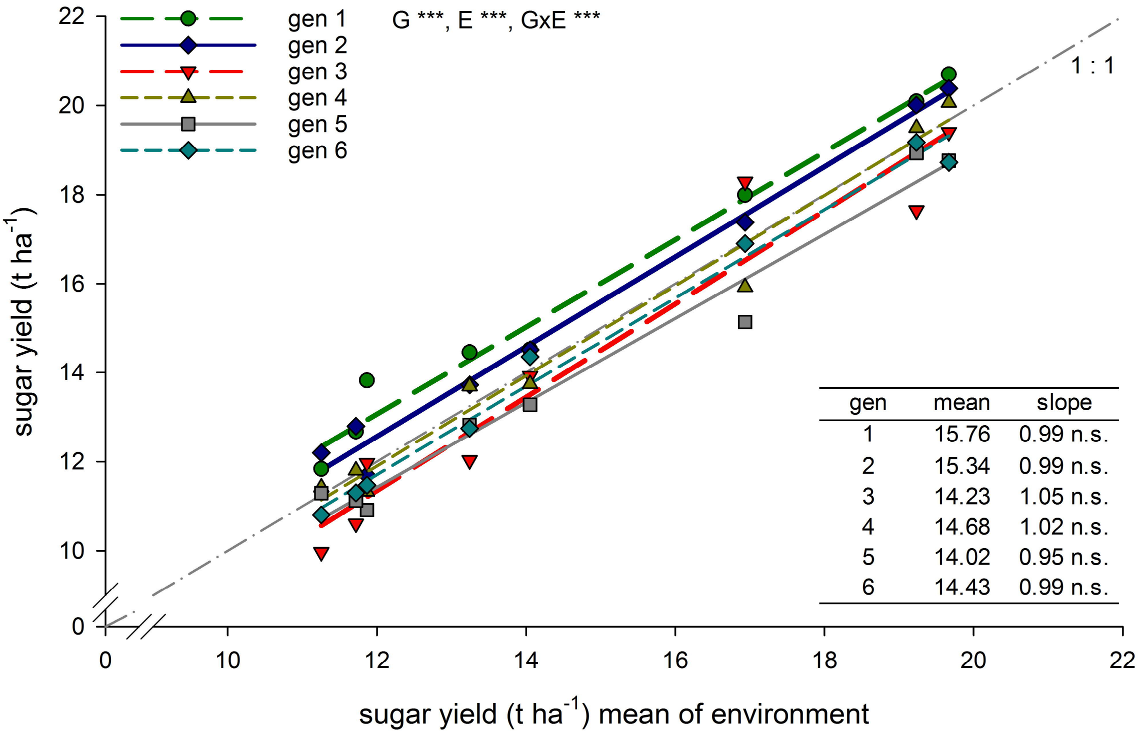


Fig. 2: Sugar yield of six sugar beet genotypes (G) in relation to the environmental mean at 8 environments (E) with field trials in Italy, France and Germany in 2018 and 2019, treatments: irrigated, non-irrigated (=drought stress); environment = site x year x treatment, *** significant at P < 0.001, for slope of regression: n.s. = not significantly different to 1.

Based on the eight environments, growing conditions were extended by adding three further environments with differences in water supply and by six environments with differences in nitrogen supply. Also for the 17 environments, sugar yield, root yield and sugar content of individual genotypes were plotted against the mean values of environments (Fig. 3 and 4). For sugar yield, effects of genotype and environment were significant (Fig. 3). The range of environmental means remained the same for 17 environments as for eight environments. On average across all environments, genotype 1 reached the highest sugar yield with 16.8 t ha^{-1}, whereas genotype 5 had the lowest sugar yield with 14.7 t ha^{-1}. Despite the significant interaction between genotype and environment, the slope of the regression lines did not differ significantly from 1, with exception of genotype 4 (1.09).

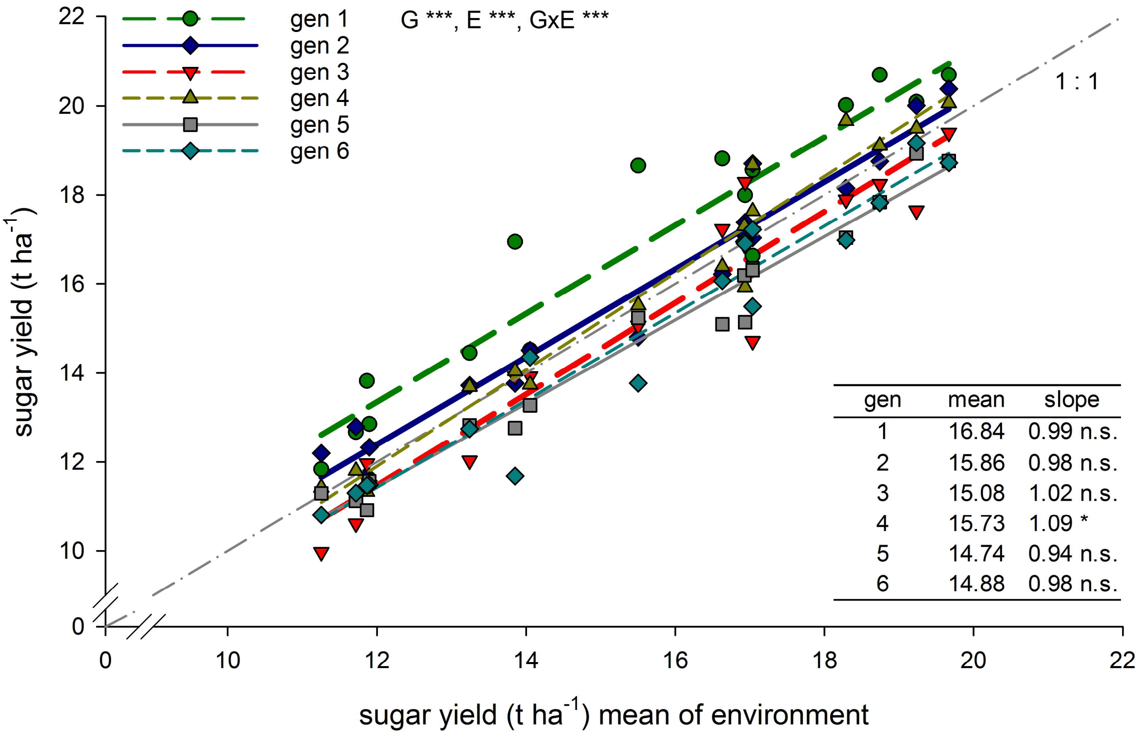


Fig. 3: Sugar yield of six sugar beet genotypes (G) in relation to the environmental mean at 17 environments (E) with field trials in Italy, France and Germany in 2018 and 2019, treatments: irrigated, non-irrigated (=drought stress), nitrogen supply of 60, 120, 240 kg N ha^{-1}; environment = site x year x treatment, *** significant at $P < 0.001$; for slope of regression * significantly different to 1 at $P < 0.05$, n.s. = not significantly different to 1.

Root yield showed significant differences between the genotypes and the environments, and also a significant GxE interaction. (Fig. 4a). The environmental mean ranged from 52.9 t ha^{-1} under unfavourable conditions to 126.8 t ha^{-1} under very favourable conditions. Averaged over all environments, genotype 1 reached the highest root yield with 95.8 t ha^{-1}, whereas genotype 6 yielded lowest with 77.3 t ha^{-1}. The interaction resulted in small differences between the genotypes under unfavourable conditions, whereas under more favourable conditions, genotype differences became more pronounced.

The sugar content showed significant differences between the genotypes and the environment, and a significant GxE interaction, too (Fig. 4b). The environmental mean ranged from 13.5 % to 21.3 %. Averaged over all environments, genotype 6 had the highest sugar content (19.4 %) and genotype 4 the lowest (17.3 %). In contrast to root yield, differences in sugar content between genotypes were more distinct at environments with low sugar content.

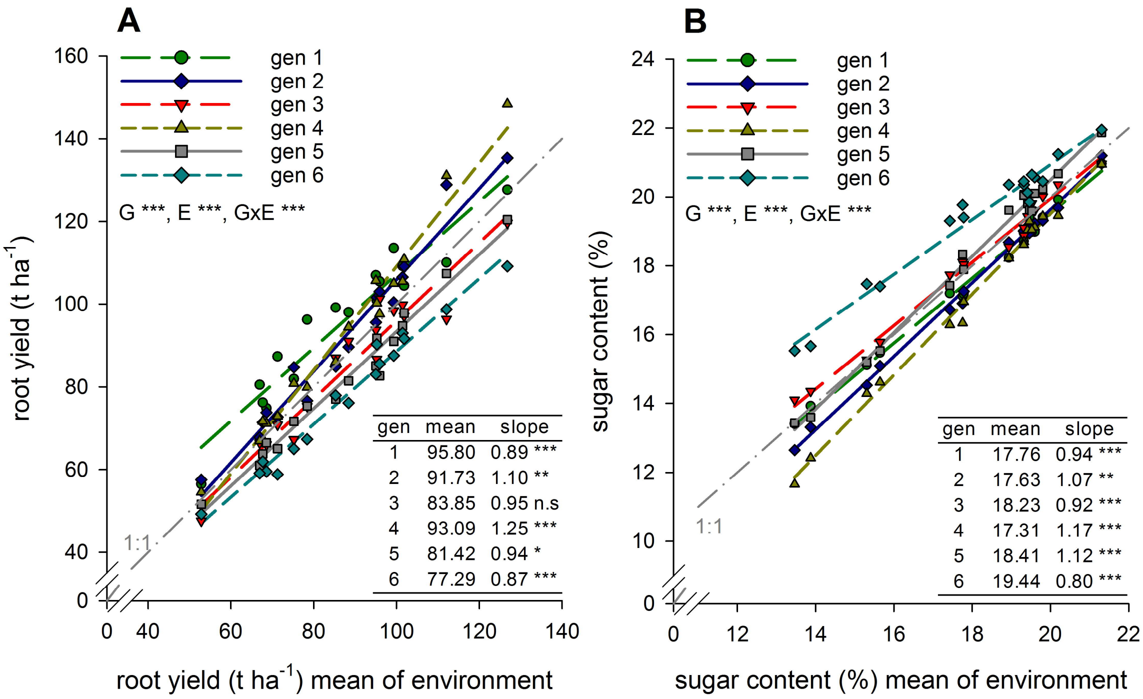
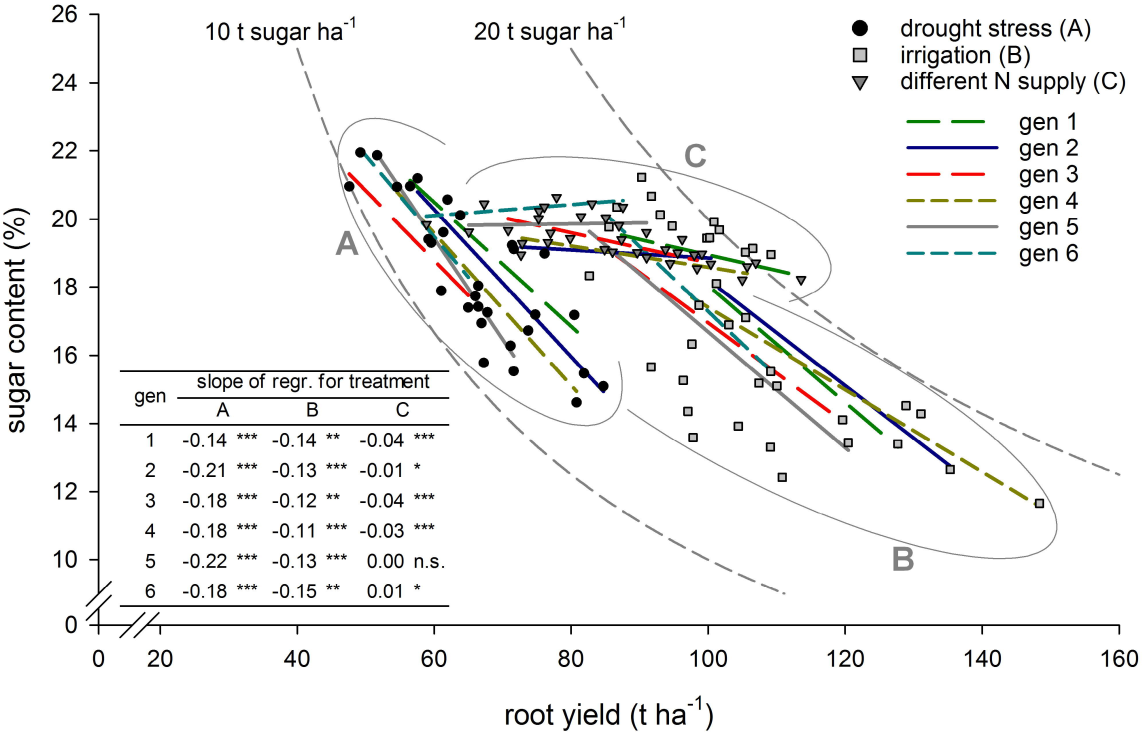


Fig. 4: Root yield (A) and sugar content (B) of six sugar beet genotypes in relation to the environmental mean at 17 environments (E) with field trials in Italy, France and Germany in 2018 and 2019, treatments: irrigated, non-irrigated (drought stress) and nitrogen supply (60, 120, 240 kg N ha^{-1}); environment = site x year x treatment, *** significant at $P < 0.001$; for slope of regression *, **, *** significantly different to 1 at $P < 0.05$, $P < 0.01$, $P < 0.001$, n.s. = not significantly different to 1.

The sugar content in relation to the root yield (covering a range of 10 to 20 t of sugar ha^{-1}) is shown for the six genotypes in 17 environments (Fig. 5). The environments were grouped according to water supply treatment (drought stress and sufficient irrigation) and N treatment (encircled). For the water supply treatments, an increase in root yield was always associated with a pronounced decrease of the sugar content, resulting in a negative slope. In environments with drought stress, root yield was lower and sugar content was higher than in environments with irrigation. In both conditions, the slope of the regression was similar for all genotypes. In environments with differences in N supply, however, a root yield increase was accompanied by a much lower decrease in sugar content than in environments with drought stress or irrigation. Therefore, the slopes of the regressions for the genotypes over the environments with different N supply were close to zero.



gen	slope of regr. for treatment		
	A	B	C
1	-0.14 ***	-0.14 **	-0.04 ***
2	-0.21 ***	-0.13 ***	-0.01 *
3	-0.18 ***	-0.12 **	-0.04 ***
4	-0.18 ***	-0.11 ***	-0.03 ***
5	-0.22 ***	-0.13 ***	0.00 n.s.
6	-0.18 ***	-0.15 **	0.01 *

Fig. 5: Sugar content and root yield of six sugar beet genotypes under drought stress (A), irrigation (B) and different N supply (60, 120, 240 kg N ha^{-1}) (C); in total 17 environments, field trials in Italy, France and Germany in 2018 and 2019, environment = site x year x treatment, regression for each genotype over all environments for the respective treatments, table indicate slope of regression significant different to 0 with *, **, *** at $P < 0.05$, $P < 0.01$ and $P < 0.001$, n.s. = not significant.

The yield stability index (YSI) considers yield potential and environmental yield stability. For sugar yield, the adjusted yield ranking and the rating of stability variance, as well as the yield stability index, are presented for the six genotypes in both 8 and 17 environments (Fig. 6a, b). In 8 environments characterised by differences in water supply, genotypes 1 and 2 reached the highest YSI. These two genotypes had a high adjusted yield ranking in combination with the highest or at least a high stability rating of 0 (genotype 2) or -2 (genotype 1). The lowest YSI of -4 for genotype 3 resulted from a low adjusted yield rank and the lowest stability rating.

Including the environments with different N supply (Fig. 6b) changed the ranking in YSI only slightly. Genotype 2 had still the highest YSI, followed by genotypes 1 and 4. Nevertheless, genotype 1 had a lower rating of stability variance and consequently lower YSI in 17 compared to 8 environments, despite maintaining the highest adjusted yield rank. Genotype 3 remained the genotype with the lowest YSI by its combination of low adjusted yield rank and lowest stability rating.

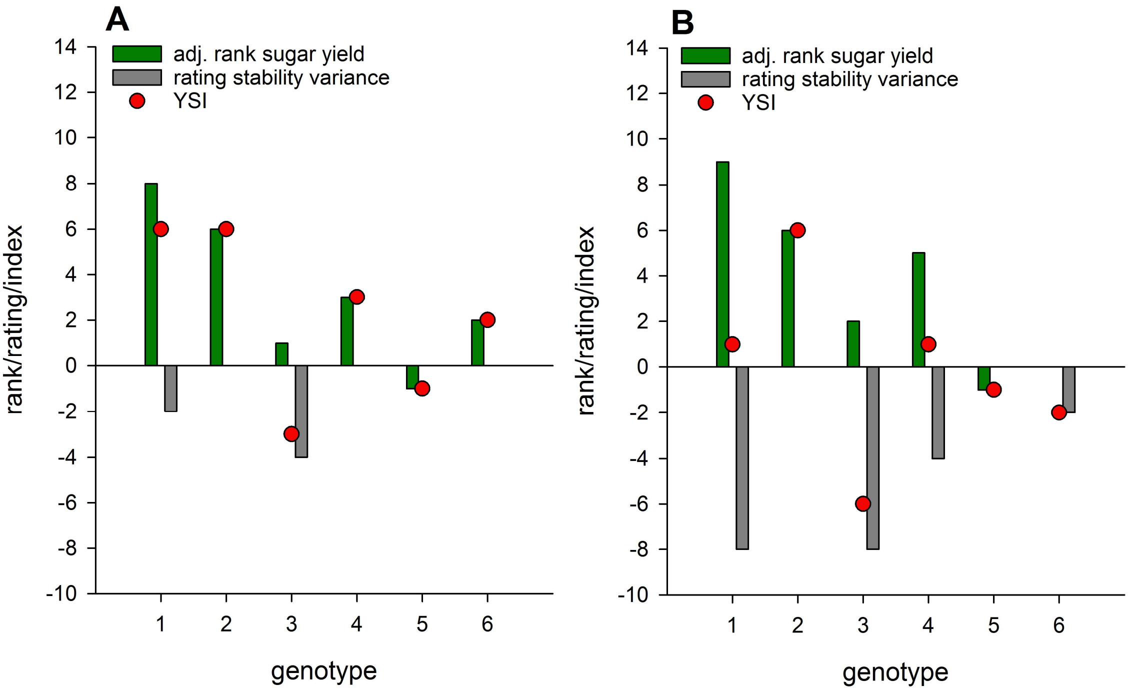


Fig. 6: Rating of stability variance, adjusted yield rank and yield stability index (YSI) according to Kang (1993) of six sugar beet genotypes (A) in 8 environments characterized by differences in water supply (irrigated, non-irrigated), and (B) in 17 environments characterized by differences in water and nitrogen supply (irrigated, non-irrigated, nitrogen supply with 60, 120, 240 kg N ha^{-1}), field trials in Italy, France and Germany in 2018 and 2019.

The relative Shukla variance in relation to the relative sugar yield is shown for the six sugar beet genotypes in 8 (varying in water supply) and in all 17 environments (varying in supply of water or N) (Fig. 7). A high variance characterises a low environmental yield stability and vice versa. Genotype 3 is located in the third quadrant for both 8 and 17 environments, where genotypes with a low yield potential in combination with low stability are classified. The yield stability increased considerably when genotype 3 was tested in 17 instead of 8 environments. Genotype 2 and genotype 4 (17 environments) are located in the first quadrant, which is characterized by a high yield potential in combination with high yield stability. Genotype 1 had the highest yield potential in both 8 and 17 environments, but its yield stability was significantly lower when all 17 environments were included.

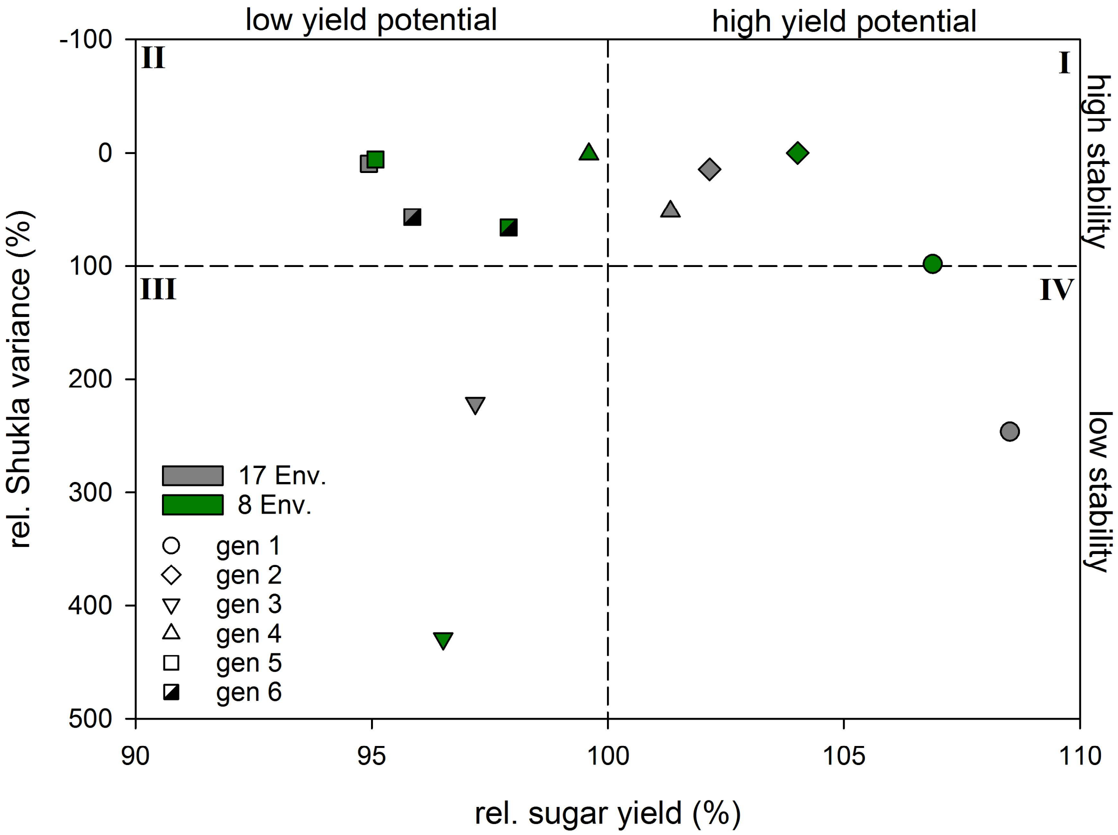


Fig. 7: Relative Shukla variance in relation to relative sugar yield of six sugar beet genotypes in 8 environments characterized by differences in water supply (drought stress, irrigation), or in 17 environments characterized by differences in water and N supply (drought stress, irrigation, N supply with 60, 120, 240 kg N ha^{-1}); field trials in Italy, France and Germany in 2018 and 2019; based on Shukla's stability variance (Shukla 1972), lower values indicate more stable sugar yields, 100 % corresponds to mean sugar yield or mean Shukla variance of all genotypes in 8 or 17 environments, respectively.

4 Discussion

The response of different genotypes to environmental conditions, in particular to drought stress, can be analyzed with different experimental approaches. Under field conditions, this has been investigated in only a few studies yet. The reaction of partially commercial varieties to different environmental conditions at various sites in UK was simulated with a crop growth model by Pidgeon et al. (2006). Hoffmann et al. (2009) chose sugar beet genotypes according to differences in the technical quality and tested them in two years at 52 sites across Europe. Similarly, Hassani et al. (2018) tested different genotypes in eight environments across Iran. However, although different environmental conditions with regard to temperature and precipitation were included, there was no direct comparison of drought stress and sufficient water supply in either study. Therefore, other reasons than drought stress may have caused differences in genotype response.

A direct comparison was carried out by Ober et al. (2004). A polythene tunnel enabled the controlled occurrence of drought stress. Two treatments, either full irrigation or no irrigation for a certain period were applied, but only under these artificial conditions at one site in three consecutive years.

In the current study, drought stress trials with a direct comparison to irrigation were carried out at sites with low precipitation and natural occurrence of drought, comprising also heat stress. Genotypes with an expected different response to drought stress were tested at three different sites in two years. In a further step of evaluation, the data set was extended by environments with differences in N supply. Hence, this is the first study to test a set of sugar beet genotypes in many environments differing in water and N availability. Therefore, these data will get greater relevance for the assessment of crop performance in field conditions and breeding (Stahl et al., 2020).

4.1 GxE Interaction

In this study, the genotypes were tested under drought stress conditions to identify those with drought tolerance. Although not all soil conditions leading to a higher frequency of drought stress occurrence such as light soils and low rooting depth could be considered in our trials, the wide range of sugar yields from 10 to 20 t ha^{-1} covers a large set of environmental conditions under which sugar beet is cultivated.

In the direct comparison between drought stress and irrigation, there was no significant interaction between genotype and irrigation treatment, although the extent of yield reduction varied with the severity of drought stress. Also in the study of Ober et al. (2004) the close correlation between irrigated and non-irrigated sugar yields in field trials indicated a lack of interaction. Hence, even in our set of genotypes with an expected different reaction to drought stress there was a similar response with regard to drought tolerance, providing no indication for a special adaptation.

However, it should be considered that the genotypes included were already improved by breeding, they were hybrids, so that the extremes in reaction might have been eliminated. Ober and Rajabi (2010) showed a greater genetic diversity in drought tolerance index in a large set of genotypes, while Ober and Luterbacher (2002) observed interactions between genotype and irrigation treatment pointing to a higher variability in traits related to drought tolerance in pre-breeding material including 30 genotypes. Also Pidgeon et al. (2006)

reported of a GxE interaction in official variety testings in England, when simulating yield in different environmental conditions with a crop growth model.

In the current study the lack of a relevant interaction results in a similar genotype ranking, independent of environmental conditions. Therefore, for the selected genotypes, it was observed that the best under irrigated conditions were also superior under drought stress conditions. This response results in a slope not differing from 1, which indicates stable genotypes and points to minor GxE interaction (Annicchiarico, 2002; Becker and Léon, 1988; Malosetti et al., 2013). However, further trials in more extreme environments with an increased number of more extreme genotypic material are needed to completely exclude the interaction.

The genotype ranking may occasionally change in individual environments, as observed in particular for genotype 3. The slope of 1.05 in the 8 environments with different water supply points to a higher yield under favorable conditions, or in the contrary, to a higher susceptibility to drought compared to the other genotypes. This change in response in different environments then resulted in the lowest yield stability. That confirms Ober et al. (2004) who also noted that the drought tolerant genotypes were those that were less able to take full advantage of optimum growing conditions.

Further environments with different conditions, not only characterized by differences in water supply, but also in N supply, were included in the evaluation. Despite the significance of the GxE interaction the effect was negligible, as also observed by Hoffmann et al. (2009) in 52 environments across Europe with large differences in soil and weather conditions. The superior genotypes were irrespective of environment the best as also observed by Ober et al. (2004) and by Abou-Elwafa and Shehzad (2020) even under drought and heat.

An explanation for this low GxE interaction could be that sugar beet is harvested in the vegetative growth stage in commercial cultivation. Different to grain crops, sugar beet crops experience no susceptible reproductive growth stages such as bolting and flowering (Hoffmann et al., 2020; Hoffmann et al., 2009), where differences in the response to drought stress arise first. In Australia, adaption of wheat and consequently improved yield was also explained with earlier flowering and maturity before the onset drought and heat (Richards et al., 2014). Another important reason for the low GxE interaction is probably, that in most growth phases sugar beet is not source limited (Hoffmann et al., 2020; Hoffmann, 2019).Therefore, it can be assumed that sugar beet can cope better with a reduction in canopy cover (triggered by drought stress) than crops that are limited by light interception. Under drought, cell expansion in the storage root as sink is the most sensitive metabolic process, much more sensitive than photosynthesis or sugar accumulation (Hsiao, 1973). As a consequence of this growth limitation, sugar is accumulated in the leaves and suggests a downregulation of photosynthesis as feedback regulation (Mäck and Hoffmann, 2006). Therefore, the assimilate supply is probably not the limiting factor (Hoffmann, 2010), but seems always high enough to maintain yield formation, even if light interception by the leaf canopy and assimilation is temporarily affected during growth (e.g. by drought stress). Hence, sugar beet is less sensitive to changes in growing conditions affecting canopy cover and can therefore provide stable yields under varying environmental conditions (Evans, 1975; Hoffmann et al., 2020), which leads to the absence of considerable GxE interaction.

Interactions between genotype and environment were observed in various studies for maize (Kang and Gorman, 1989; Ribaut et al., 1997; Ribaut et al., 1996), soybeans (Cucolotto et al., 2007; Yan et al., 2010) and cereals (Patterson et al., 1977; Weber and Westermann, 1994). However, when tested in the absence of diseases due to full agronomic intensity, a close correlation between the irrigated and non-irrigated treatment occurred for 191 wheat genotypes at one site (Voss-Fels et al., 2019). This indicates that GxE interactions may often occur because of differences in disease tolerance, but not necessarily in yield performance.

GxE interactions in sugar beet due to the infestation with diseases were described by Laufer et al. (2020) and Märländer et al. (2018). Especially dry and warm conditions in combination with occasional precipitation and high humidity are favorable for the infestation with the leaf spot disease *Cercospora beticola* Sacc. (Windels et al., 1998). The occurrence of Cercospora is therefore often higher under irrigation. Different levels of resistance or tolerance towards diseases can cause GxE interactions and thus changes in genotype ranking. This might be misinterpreted as genotypic difference in drought tolerance, when impact factors are not separated precisely.

Recently Snowdon et al. (2020) reported that long-term genetic gains were achieved through conventional breeding which has increased crop yields through accumulation of beneficial, small-effect variants. Along with the increased yields better stress adaptation and yield stability under abiotic stress constraints were obtained. However, the authors found that source-sink trade-offs often counter the improvement of single yield components, pointing to the need of a holistic view on crop yield formation, also under drought.

4.2 Relation between root yield and sugar content

Under drought stress, the reduction in root yield was always accompanied by a considerable increase in sugar content. Hence, the obvious reduction in root yield in response to drought stress does not allow final conclusions about the level of sugar yield, as lower root yield is compensated by higher sugar content; under conditions with sufficient water, it is vice versa, as also observed in trials in 52 different environments (Hoffmann et al., 2009). Surprisingly, this negative correlation between root yield and sugar content was similar for all genotypes independent of their expected differences in drought tolerance in a wide range of sugar yields. This phenomenon was already observed in previous studies (Allison et al., 1996; Artschwager, 1926; Doney et al., 1981; Milford, 1973), but is now confirmed for a great range of genotypes and environments.

The reason for this negative correlation is probably the reduced water content in the storage root cells under drought, so that sugar gets concentrated while root yield declines (Bloch et al., 2006; Milford, 2006). This seems to be a universal correlation for sugar beet irrespective of yield potential and yield type of the genotypes (similar slope). In drought stress environments, which constitute less favorable growth conditions, sugar contents are higher, while under irrigation and thus more favorable growth conditions, higher root yields are achieved. The maximum distinction between genotypes in both sugar content and root yield occurred under favorable growth conditions with adequate water supply. Such environments are most discriminating to select genotypes superior in one of these traits, which characterize the different types of sugar beet varieties (Bosemark, 1993).

In environments with varying N supply, the relation between sugar content and root yield was slightly different. Increasing N supply and thus root yield did not reduce the sugar content as much as irrigation. High N supply leads to increased plant growth, and at least up to the optimum N supply, to increased root dry matter. Assimilates, which are consumed for growth, are used at the expense of sugar storage and thus sugar content (Milford and Watson, 1971). On the other hand, there is a presumed surplus of assimilates, because sugar beet are sink limited (Hoffmann, 2019). In addition to the only little changes in the water content of the root tissue, this is probably the reason why genotypes responded with rather constant or only slightly decreasing sugar content to increasing root yield in the environments with different N supply. But in N response, differences between the genotypes occurred. In particular, genotype 1 showed a higher reaction to N supply than the other genotypes.

Possibly reasons such as differences in N uptake or N use efficiency have to be studied in more detail.

4.3 Relation between yield potential and yield stability

For cultivation, high yield potential in combination with high environmental yield stability (=low variance between environments) would be optimal. Genotypic differences in stability for sugar yield occurred in this study. Genotypes 1 and 3 varied in yield stability depending on whether the environments differed in water supply or in addition also in N supply, corresponding to the differences in yield response. However, it may demonstrate that a lower yield stability is not necessarily negative: Genotype 1 showed a strong reaction to N supply with a higher yield increase than the other genotypes, which is reflected in a higher variance and thus lower stability.

Genotypic differences in yield stability were also observed for sugar beet in studies of Tsialtas et al. (2014), as well as for maize and cereals (Changizi et al., 2014; Helms, 1993; Roostaei et al., 2014). In these studies, yield stability was not at all or only slightly correlated to the yield potential. This is confirmed in our study, where all combinations of high and low yield potential and yield stability occurred. Because of this lack of correlation, environmental yield stability of a genotype cannot be deduced from its yield potential. For the determination of yield stability multi-annual trials under different environmental conditions are required.

5 Conclusions

In the absence of diseases, no relevant GxE interaction occurred for sugar yield in this study, so there was no indication of a special adaption to drought stress. The sugar yield potential can be taken as the relevant trait for selection. If the genotype with the highest sugar yield is selected, this genotype will be superior under all environmental conditions (as long as no diseases occur).

This demonstrates that for breeding of sugar beet varieties less test environments are required compared to grain crops, which might simplify the breeding process. Because of the GxE interaction for root yield and sugar content, test environments characterized by sufficient water supply are most discriminating for these traits.

Beside high yield potential, varieties should also be characterized by high environmental yield stability, which is calculated from the variance. Therefore, different test environments are required to cover the variance representatively. Despite the generally high yield stability of sugar beet, genotypic differences occurred in this study. Whether in variety selection and consequently cultivation more priority should be given to yield potential or yield stability depends on the environment, in which the variety will be grown. Under stable environmental conditions, such as those mostly prevailing in Northern and Central Europe, the focus can probably be put more on yield potential than on yield stability. In future, however, climatic changes are expected to result in more periods of drought and heat (IPCC, 2013), most likely often associated with higher pressure of pests and diseases. Against this background, in the future development of varieties greater attention should be paid to yield stability, including disease tolerances as well.

Authorship contributions

Conception and design of study: C.M. Hoffmann, K. Fiedler-Wiechers. Acquisition of data: H. Ebmeyer, K. Fiedler-Wiechers. Analysis and/or interpretation of data: H. Ebmeyer, C.M. Hoffmann. Drafting the manuscript: H. Ebmeyer, C.M. Hoffmann. Revising the manuscript critically for important intellectual content: C.M. Hoffmann, H. Ebmeyer, K. Fiedler-Wiechers. Approval of the version of the manuscript to be published: H. Ebmeyer, K. Fiedler-Wiechers, C.M. Hoffmann.

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Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Manuskript III

Efficiency of nitrogen uptake and utilization in sugar beet genotypes[3]

HENNING EBMEYER, CHRISTA M. HOFFMANN

Abstract

The nitrogen use efficiency (NUE) is composed of the nitrogen uptake (NUpE) and nitrogen utilization efficiency (NUtE). The contribution of these components to overall NUE of sugar beet genotypes is unknown, as well as the reasons for genotypic variation. In 2018 and 2019, 6 genotypes were studied in field trials at three N levels (65, 120, 240 kg N ha^{-1}). The trials revealed only minor genotypic differences in N uptake and N uptake efficiency, but distinct genotypic differences in N utilization efficiency and NUE. The interaction between genotype and environment was negligible, i.e. differences between genotypes in NUE were independent of N management, and there was no genotypic adaptation to low N availability. Differences in NUE resulted rather from differences in sugar yield potential. This demonstrates that selection to high sugar yield potential will also promote NUE. It was concluded that a high sugar yield potential resulted from an assimilate partitioning towards high sugar yield, in combination with a low leaf mass to total dry mass ratio. There was evidence that lower leaf mass resulted in higher levels of leaf N content. If a higher leaf N content could be used to identify high yielding genotypes is unclear, but it was concluded that a high leaf mass is not a prerequisite for high sugar yields.

Keywords

NUE, sugar yield potential, assimilate partitioning, leaf mass, N content

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1 Introduction

Resource availability is a major constraint to yield increase in many cropping systems, so that the efficient use of resources such as nitrogen is always of importance (Sinclair and Rufty, 2012). In contrast to many other crops, sugar beet is rather efficient in the use of resources, also in terms of nitrogen use (Hoffmann and Stockfisch, 2010). One reason might be that sugar beet can nearly completely extract mineral nitrogen from the soil (Armstrong et al., 1986). Water shortage as result of climate change with more frequent periods of drought could restrict nutrient flux towards the roots and nutrient uptake by the plants (Ehlers and Goss, 2003). There are approaches of newer technology using microbial inoculants to promote the uptake of nutrients from fertilizers and soil stocks to improve water uptake and to fix atmospheric nitrogen through microbial organisms (Schütz et al., 2017; Turan et al., 2019). However, the lowest response of NUE on this newer technology was obtained in root crops, including sugar beet (Schütz et al., 2017). Therefore, other possibilities to achieve high nitrogen use efficiency (NUE) of sugar beet is gaining importance. For the development of cultivars with high NUE a comprehensive understanding of its components N uptake efficiency (NUpE) and N utilization efficiency (NUtE) (Moll et al., 1982) is needed. Their individual contribution to the overall NUE appears to depend on crop type (Chakwizira et al., 2014).

For cereals and maize, genotypic variation in NUE was found (Beatty et al., 2010; Bertin and Gallais, 2000; Gaju et al., 2011; Le Gouis et al., 2000). Differences in the rooting capacity of wheat genotypes were associated with nitrogen acquisition under restricted N supply, leading to differences in NUpE (Ford et al., 2006; Gaju et al., 2011). Gaju et al. (2011) concluded that delaying leaf senescence after flowering could maintain longer assimilate supply in wheat, thus increasing yield and NUtE. For maize, there is evidence that differences in the regulation of kernel set, i.e. in sink restriction, lead to differences in yield and NUE (Paponov et al., 2020). These results point to a contribution of both source and sink to differences in NUE.

Furthermore, these reports emphasize that NUE of cereals and maize can be improved by breeding. The reason may be that for cereals N is stored in the harvestable plant organ in the form of protein (Spiertz and Vos, 1983). This creates a high demand for N in phases such as grain filling, but also flowering and shooting (Cliquet et al., 1990; Masclaux-Daubresse et al., 2010).

Sugar beet, in contrast, do not have periods like bolting or flowering with particularly high N demand (Hoffmann et al., 2020; Hoffmann et al., 2009). Also, the main harvest product is sugar, which does not contain N. In sugar beet, high N supply primarily promotes leaf formation (Malnou et al., 2008). It is not clear whether an enlarged leaf canopy with higher light interception can result in higher yields, and consequently in an increased NUE.

For sugar beet the N uptake and NUpE as well as the NUtE have already been investigated in several studies. It was observed that N supply is important for the development of leaf canopy in the early growth period, and less relevant for yield formation in later growth stages (Laufer and Koch, 2017; Malnou et al., 2008). High amounts of N supply shifted dry matter partitioning towards leaf growth without increasing the total dry matter (Laufer and Koch, 2017; Milford and Watson, 1971). It is not known whether there are genotypic differences in dry matter partitioning and if this can improve the NUE. A comparison of sugar and fodder beet pointed to improvements of NUtE due to breeding effort towards higher sugar yield (Laufer et al., 2016). However, it remains to be examined whether there are also differences among sugar beet genotypes.

Latest studies show that in sugar beet the water use efficiency (WUE), which represents yield relative to water consumption, is largely determined by the sugar yield potential (Ebmeyer and Hoffmann, submitted). Whether this is similar for NUE, and which factors might influence the NUE of sugar beet, is not clear yet.

The objective of the current study was thus to analyze the components of NUE of sugar beet, NUpE and NUtE, and to identify reasons for genotypic variation. Furthermore, it was investigated if a large leaf canopy is a prerequisite for high sugar yields.

2 Material and methods

2.1 Experimental design

In 2018 and 2019, six sugar beet genotypes (*Beta vulgaris* L. spp.) were tested in field trials with different amounts of nitrogen (N) fertilizer on a Luvisol from loess (silty loam) near to Göttingen, Lower Saxony, Germany (2018: 51°27'57.9"N 9°54'59.6"E; 2019: 51°28'10.5"N 9°54'22.6"E). In both years, the soil had a pH of 6.8-6.9 and soil organic carbon content of 1.2-2.4%. The six genotypes were hybrids from one breeder, and were tolerant against rhizomania. They were selected to represent a range of different yield-types with either high sugar content, high root yield or high marc content, and putative drought tolerance as mentioned by Ebmeyer et al. (2021). Therefore, genotypes were not selected with regard to differences in NUE.

Different amounts of calcium ammonium nitrate were added to a supply of 65, 120 and 240 kg N ha^{-1}, including the soil mineral N content at sowing (approx. 65 kg in 0-90 cm in both years). According to good agricultural practice approx. 80-100 kg N ha^{-1} are applied in this region. Application of N fertilizer was done by hand. The highest treatment (240 kg N ha^{-1}) was split into two doses (after sowing, at 4-6 leaves stage) to avoid salt stress. Genotypes and N treatments were completely randomized in a two factorial block design with four replicates. Plots included nine rows of 8 m length with 0.45 m row distance, of which rows 2, 3, 4 were harvested in July and rows 6, 7, 8 in October. The outer rows (1, 5, 9) served as border to avoid neighboring effects. Sugar beet plants were sown in April and harvested in October, 175 (2018) or 183 (2019) days after sowing.

A population of 90.000 plants ha^{-1} was achieved by manual thinning. Plant protection measures were carried out according to the local standard to control weeds, pests, and diseases. No infestation with leaf diseases occurred.

In both years, the amount of precipitation and air temperature differed from the long-term average 1981-2010 (Fig. 1). Precipitation was considerably below the long-term average in both years. In January 2018 and May 2019, it was distinctly above average. In May 2019, this resulted from an extreme weather event with 76 mm in 24 h. Air temperature was considerably higher than average, especially at the beginning of the season in April 2018.

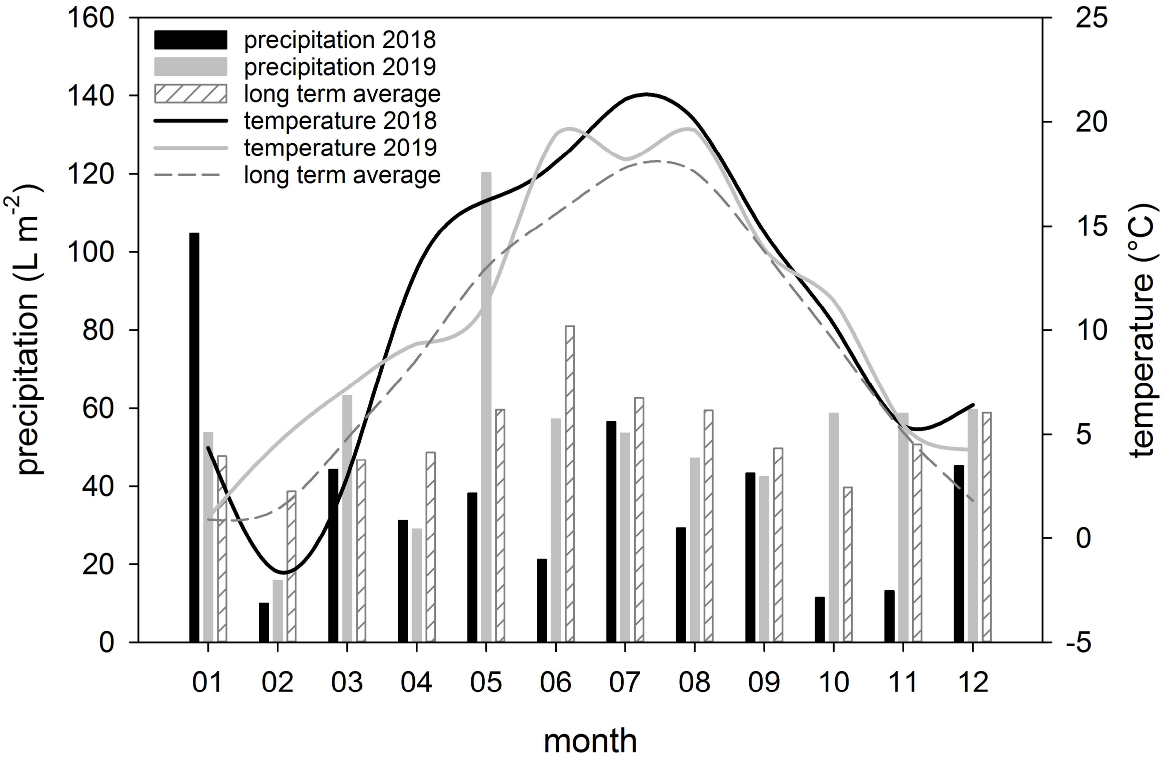

Fig. 1: Precipitation and air temperature at the trial site in Göttingen in 2018 and 2019, long-term average 1981–2010, one event with 76 L m^{-2} in 24 h on 20 May 2019.

2.2 Harvest and sample analyses

Sugar beet plants of three rows (10.8 m²) were hand lifted and subsequently leaves were separated from the storage root below the green leaf scars. Leaves including the tops were weighed in the field and a representative sample was taken. Leaves of ten plants were separated into young and old leaves. These fractions were weighed, and samples were taken of each fraction. In a central tare house, leave samples were mashed and dried at 105 °C for 24 hours for the determination of dry matter content. Equally, storage roots were washed, weighed to determine the root yield, and processed to a homogenous brei. One part of root brei was shock frozen at -70 °C and stored at -26 °C until analysis. The other part was used for the determination of dry matter content.

Beet brei samples were analyzed with an automated analyzer (Anton Paar OptoTec, Germany) after clarification with 0.3% aluminum sulphate solution in a central quality laboratory. Sugar content in the beet brei filtrates was determined polarimetrically (ICUMSA, 1994).

Nitrogen content of leave and storage root dry matter was determined by dry combustion using an element analyzer (Thermo Fisher Scientific, FlashEA 1112, USA).

2.3 Calculations

Sugar yield was calculated from root yield and sugar content of the root. Relative sugar yield and relative leaf yield is the yield in relation to the grand mean of all genotypes and N treatments in 2018 and in 2019. Nitrogen uptake in leaves and storage root was calculated from the dry matter yield and the nitrogen content of the respective fraction. Total plant nitrogen uptake is the sum of leaf and storage root N uptake.

The nitrogen use efficiency (NUE) is composed of N uptake efficiency and N utilization efficiency according to Moll et al. (1982). Thereby, the N uptake efficiency (NUpE) is defined as total plant N uptake in relation to N supply (N_{supl}) (Eq. (1)), the N utilization efficiency (NUtE) is defined as sugar yield (SY) in relation to total plant N uptake (N_{upt}) (Eq. (2)). NUE is thus defined as sugar yield in relation to N supply (Eq. (3)). The N supply is the sum of N available in the soil at sowing (N_{min}) and the amount of applied N fertilizer.

$$NUpE = N_{upt}/N_{supl} \tag{1}$$

$$NUtE = SY/N_{upt} \tag{2}$$

$$NUE = (N_{upt}/N_{supl}) \times (SY/N_{upt}) = SY/N_{supl} \tag{3}$$

2.4 Statistics

The program SAS Version 9.4. (SAS Institute Inc., Cary, NC, USA) was used for statistical evaluation of the data set. Data were checked for variance homogeneity and normal distribution (Kozak and Piepho, 2018). An analysis of variance (ANOVA) was carried out using SAS proc mixed with REML method and posthoc Tukey-Test ($\alpha \leq 0.05$). The factors genotype and N supply were regarded as fix, the factor year was regarded as random. Regression analyses were conducted with the program SigmaPlot 14.0 (Systat Software Inc., Chicago, IL, USA). Results are presented as bar charts with standard deviation for the two years separately because of the differences in weather conditions in both years. Significant effects were indicated with *, **, *** for error probabilities of $p \leq 0.05$, 0.01 and 0.001, n.s. = not significant.

3 Results

The N uptake in root and leaves increased significantly with increasing N supply (Fig 2a). For the three levels of 65, 120 and 240 kg N ha^{-1} the mean uptake amounted to 73, 87 and 114 kg N ha^{-1} in leaves and 95, 110 and 135 kg ha^{-1} in roots.

Genotypic N uptake varied from 108 to 122 kg N ha^{-1} in the storage root and from 85 to 98 kg N ha^{-1} in the leaves averaged over N supply and years (Fig. 2b). Total plant N uptake was significantly higher for genotype 1 compared to genotypes 2 to 6, which did not differ significantly. No interaction between genotype and N supply occurred.

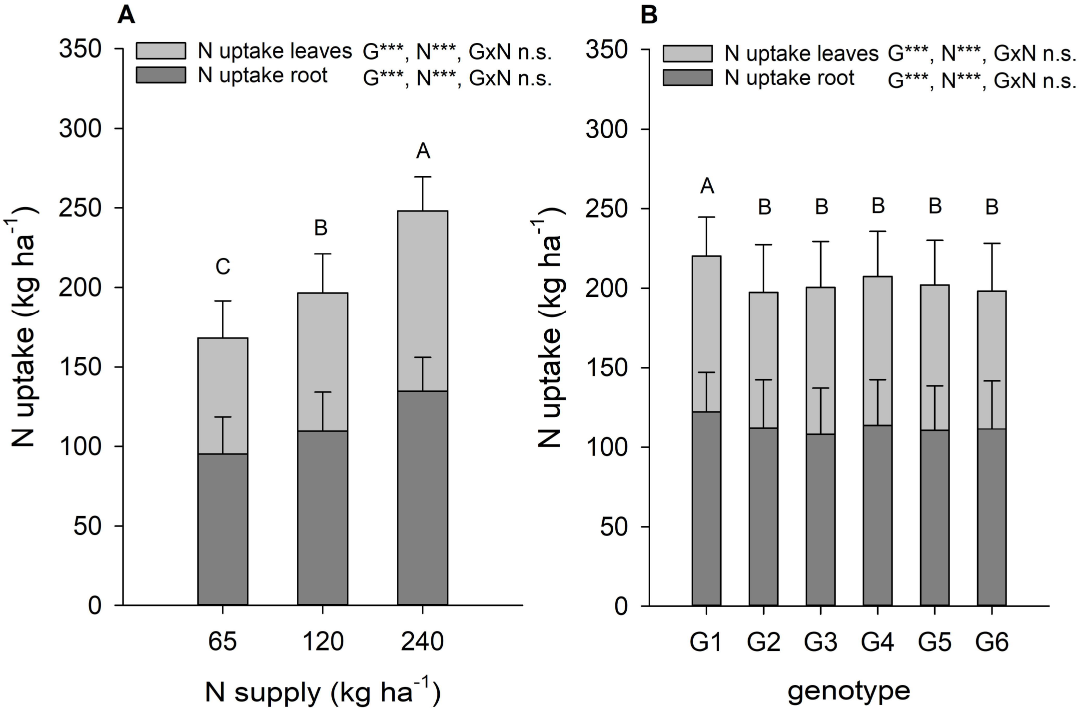

Fig. 2: N uptake in leaves and storage root of sugar beet in relation to N supply (mean of genotypes) (A) and genotype (mean of N levels) (B), mean of field trials in 2018 and 2019 in Göttingen, 6 genotypes (G), N supply (N) 65, 120 or 240 kg ha^{-1}, *** significant at $P < 0.001$, n.s. not significant, means indicated with a common letter are not significantly different, $\alpha = 0.05$ (Tukey-test).

The mean genotypic N uptake efficiency (NUpE) was higher in 2018 (1.9-2.1 kg N kg^{-1} N supply) compared to 2019 (1.4-1.8 kg kg^{-1}) (Fig. 3). In 2018 no genotypic differences occurred, whereas in 2019 genotype 1 had a significantly higher NUpE than genotypes 2 to 6. There was no genotype by N supply interaction in either year.

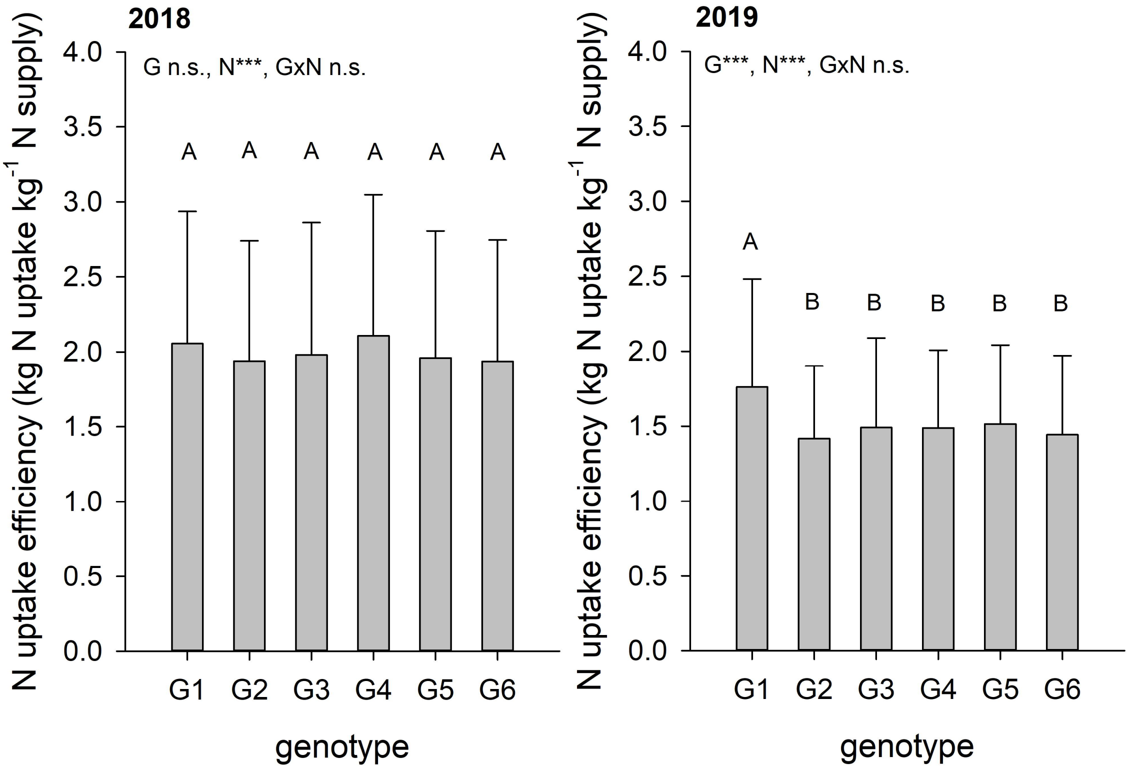

Fig. 3: Nitrogen uptake efficiency (NUpE) of 6 sugar beet genotypes (G), mean of 3 N levels (65-240 kg ha^{-1}) (N), field trials in 2018 and 2019 in Göttingen, 175 or 183 days growth, *** significant at $P < 0.001$, n.s. not significant, means indicated with a common letter are not significantly different, $\alpha = 0.05$ (Tukey-test).

The sugar yield varied among the genotypes averaged for N supply from 16.7 to 19.8 t ha^{-1} (2018) and 13.8 to 18.1 t ha^{-1} (2019) and was thus higher in 2018 than in 2019 (Fig. 4). In both years, significant differences between the genotypes occurred with similar genotype ranking. Genotype 1 had the highest, genotypes 5 and 6 the lowest sugar yield. No genotype by N supply interaction occurred in 2018. Whereas in 2019, a significant interaction occurred which was due to a slightly different response of genotypes 3 and 6 with 240 kg N supply (not shown).

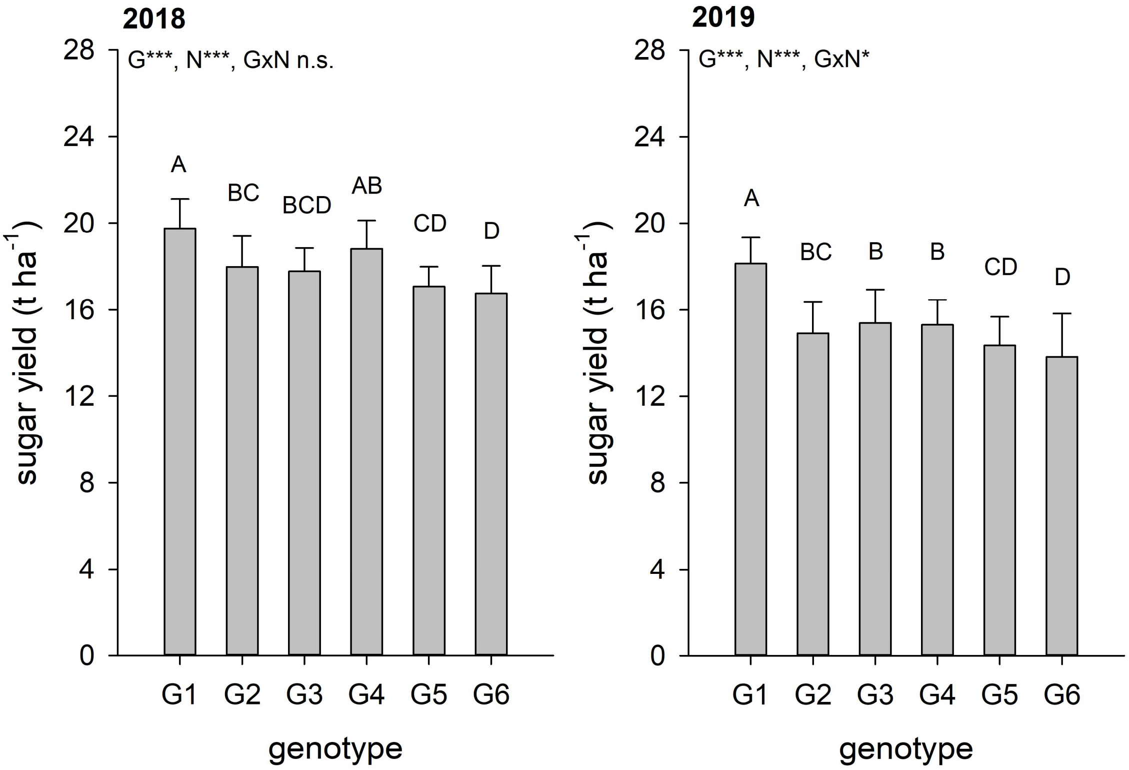

Fig. 4: Sugar yield of 6 sugar beet genotypes (G), mean of 3 N levels (65-240 kg ha^{-1}) (N), field trials in 2018 and 2019 in Göttingen, 175 or 183 days growth, *, *** significant at $P < 0.05$ or $P < 0.001$, n.s. not significant, means indicated with a common letter are not significantly different, $\alpha = 0.05$ (Tukey-test).

Sugar yield in both July and October increased with increasing total plant N uptake (Fig. 5). The regression curves of the single genotypes reached their maxima at 160 to 180 kg total plant N uptake for harvest in July and at 220 to 260 kg for harvest in October. At both harvest dates, genotype 1 yielded higher than the other genotypes. Genotypes 5 (both harvests) and 6 (October harvest) always yielded lowest. The NUtE indicating sugar yield related to total plant N uptake significantly differed among genotypes without a significant interaction between genotype and N supply.

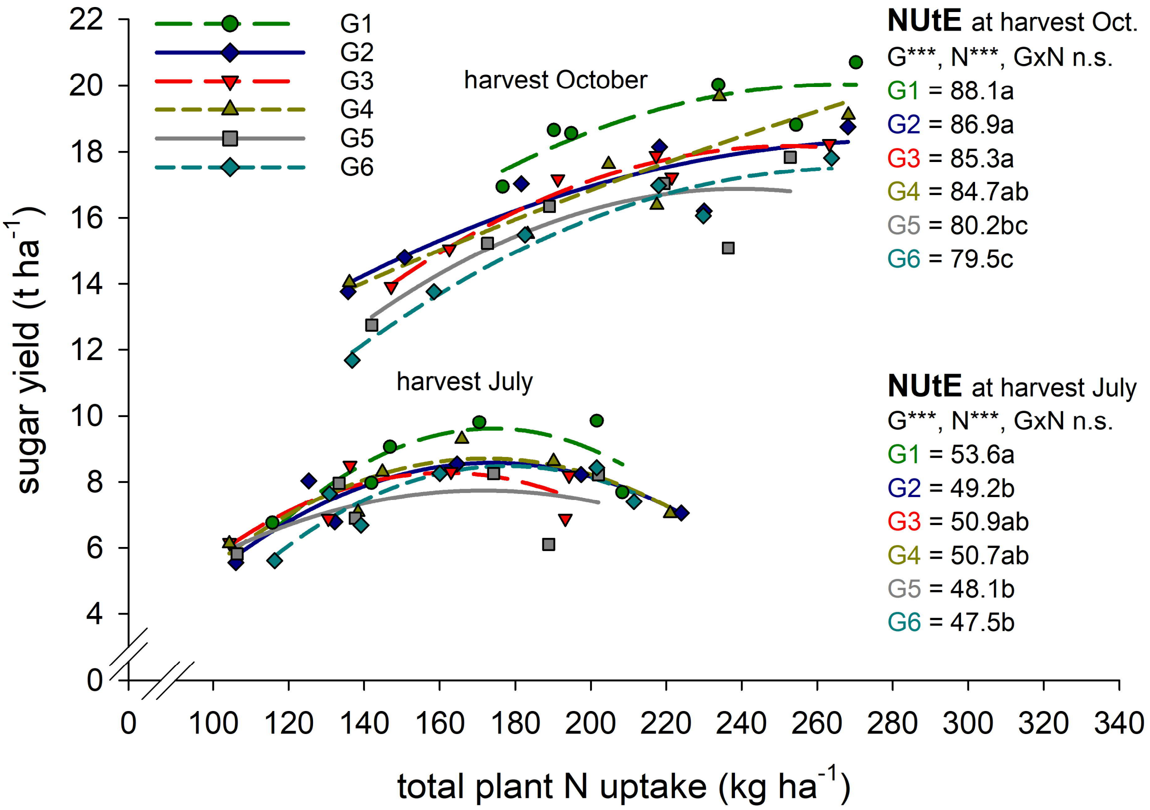

Fig. 5: Sugar yield of sugar beet harvested in July and October in relation to total plant N uptake (N utilization efficiency NUtE), mean of field trials in 2018 and 2019 in Göttingen, 6 genotypes (G), N supply (N) 65, 120, 240 kg ha^{-1}, 175 or 183 days growth, *** significant at $P < 0.001$, n.s. not significant, mean genotypic NUtEs indicated with a common letter are not significantly different, $\alpha = 0.05$ (Tukey-test).

Nitrogen use efficiency (NUE) varied among the genotypes from 153.9 to 182.5 kg kg^{-1} (2018) and 118.7 to 162.2 kg kg^{-1} (2019) and was higher in 2018 than in 2019 (Fig. 6). Significant differences between the genotypes occurred. Genotype 1 had the highest, genotype 6 the lowest NUE. The other genotypes were intermediate. No interaction between genotype and N supply occurred in 2018, whereas in 2019 the interaction was significant.

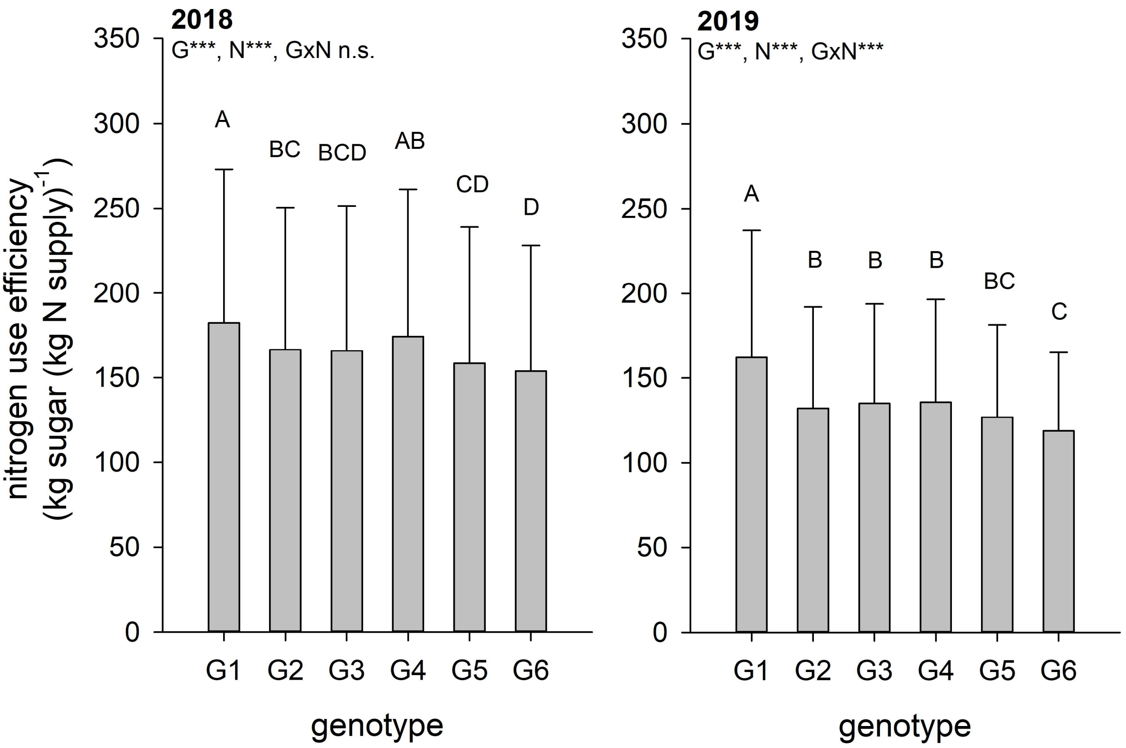

Fig. 6: Nitrogen use efficiency of 6 sugar beet genotypes (G), mean of 3 N levels (65-240 kg ha^{-1}) (N), field trials in 2018 and 2019 in Göttingen, 175 or 183 days growth, *** significant at $P < 0.001$, n.s. not significant, means indicated with a common letter are not significantly different, $\alpha = 0.05$ (Tukey-test).

The largest fraction of the total plant dry matter (DM) was sugar, varying from 59% to 65% (2018) and from 60% to 66% (2019) across all N levels (Fig 7). In both years, the same genotype ranking occurred with significant genotypic differences. Genotype 1 had the highest proportion of sugar of total DM, and genotype 5 had the lowest.

The proportion of leaf (including the tops) to total DM varied from 20% to 25% (2018) and from 19% to 25% (2019) with significant differences among genotypes and similar ranking in both years. Genotype 1 had the lowest and genotype 5 the highest proportion of leaf to total DM in both years.

There was no interaction between genotype and N supply for sugar or leaf fractions of total DM in either year.

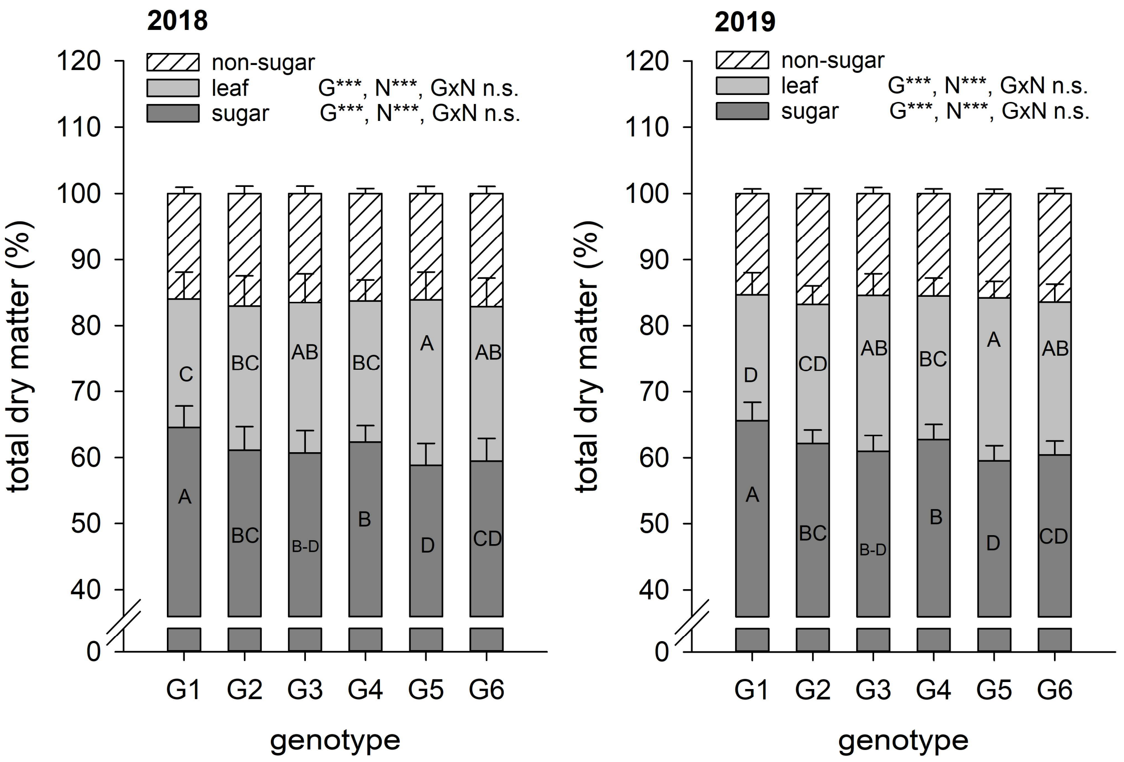

Fig. 7: Fractions of total dry matter (leaf, sugar and non-sugar in storage root) of 6 sugar beet genotypes (G), mean of 3 N levels (65-240 kg ha^{-1}) (N), field trial in 2018 and 2019 in Göttingen, 175 or 183 days growth, *** significant at $P < 0.001$, n.s. not significant, different letters indicate significant differences between genotypes for the respective fraction, $\alpha = 0.05$ (Tukey-test).

The genotypic leaf N content averaged over the N levels ranged for young sugar beet leaves from 3.0% to 3.7 %, for old leaves from 2.0% to 2.5 % (Fig. 8). Irrespective of the leaf age, the relative sugar yield increased with increasing leaf N content, whereas the relative leaf yield decreased. The regression was significant for sugar yield and for leaf yield, for both young and old leaves.

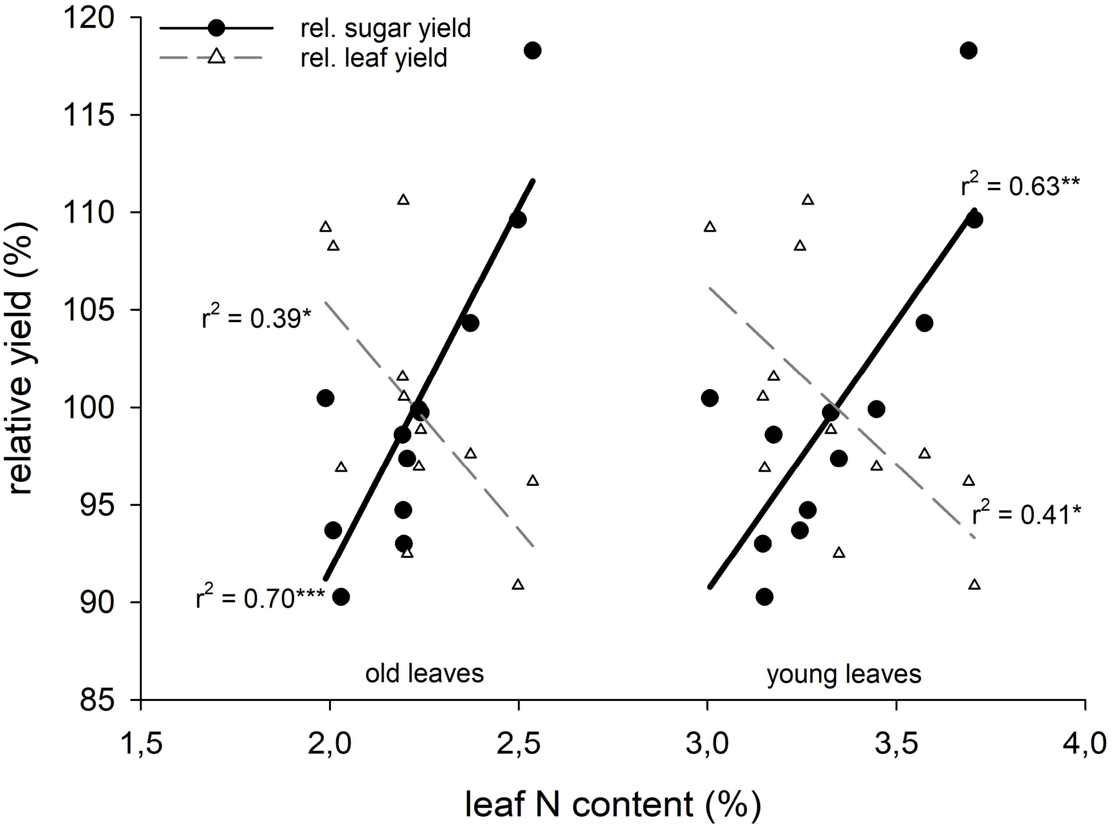

Fig. 8: Relative sugar yield and relative leaf yield in relation to the N content of young and old sugar beet leaves, field trials in Göttingen in 2018 and 2019, mean of 3 N levels (65-240 kg ha^{-1}), 6 genotypes, *, **, *** significant at $P < 0.05$, $P < 0.01$ or $P < 0.001$.

4 Discussion

4.1 Impact of temperature and precipitation

The trials of the current study differed in both years regarding weather conditions. Temperature was higher in 2018 than in 2019, especially in April and May. This probably promoted the early growth of sugar beet, resulting in higher sugar yields in 2018. Although precipitation was below the long-term average in both years, the 2018 crop benefited from water reserves in deeper soil layers from the high precipitation in the previous winter. Due to low precipitation, especially in autumn and winter 2018, the water reserves in deeper soil layers could not be replenished. This lack of water, beside cooler temperature in spring, has probably resulted in lower sugar yields in 2019. Most of the water from the extreme rainfall event in May 2019 (76 L m^{-2}) most likely ran off because the soil's water absorbency was limited due to the drought, leaving only a minor part available to the crop.

4.2 N uptake and N uptake efficiency (NUpE)

The N uptake efficiency (NUpE) is a component of the NUE and is defined as the N uptake in relation to the N supply. Genotypic variation was observed in N uptake efficiency for maize and wheat (Li et al., 2017; Zhang et al., 2020). In the current study for sugar beet, the N uptake was in the same range as observed in other studies with sugar beet (Laufer et al., 2016; Laufer and Koch, 2017; Malnou et al., 2008). While Gastal and Lemaire (2002) concluded that N uptake is determined by both N supply and crop growth (N demand), Armstrong et al. (1986) and White et al. (2016) deduced that N uptake is mainly determined by the growth rate. In the early growth period of sugar beet, temperature and radiation account for the variation in N uptake (Armstrong et al., 1986). The higher N uptake in 2018 can therefore be explained by higher temperatures and thus enhanced growth in April and May 2018 and by better water availability than in 2019 (Gonzalez-Dugo et al., 2010). This is in accordance with Badr et al. (2012), who observed for potato under varying water and N supply the lowest N uptake for the water deficit plants, which was explained by reduced N availability due to the water deficit during a period with high N demand.

Despite different weather conditions in both years, no genotypic differences in N uptake occurred in the current study except for genotype 1. For wheat under two different N supply levels, Le Gouis et al. (2000) concluded that genotypic variation in N uptake was mainly caused by grain N. In addition, genotypic differences in timing of bolting or flowering leading to a mismatch between the period of high N demand and sufficient N supply were considered as possible contributors to this genotypic variation in N uptake. For sugar beet, the generally lower genotypic variation may be explained by the absence of growth stages susceptible to inadequate N supply. As a biennial crop, sugar beet in commercial cultivation is harvested in the vegetative growth stage, so there are no susceptible growth stages such as bolting or flowering (Hoffmann et al., 2020; Hoffmann et al., 2009). A further reason might be that N is not a component of sugar as the main storage product (Hoffmann et al., 2005).

Accordingly, genotype 1 was the only one with a significantly higher NUpE in 2019, while the other genotypes did not differ. There is evidence that a variation in root characteristics can influence the N uptake, e.g. in maize (van Noordwijk et al., 1992). Therefore, the NUpE is influenced by the ability of the root to take up nutrients in many crops (Bouchet et al., 2016; Rathke et al., 2006). This is of particular importance for nutrients with a low mobility in the soil (Sattelmacher et al., 1994).

Sugar beet has generally a lower root length density than cereals or oilseed rape (Brown and Biscoe, 1985; Windt and Märländer, 1994), suggesting a higher influence of the root system on N uptake and hence also on NUpE. But despite the smaller root system, sugar beet is able to completely exhaust the N from the soil in the early growth period (Armstrong et al., 1986). However, the prerequisite for this is also an adequate supply of other nutrients (Pogłodziński et al., 2021). As the root system was not investigated in this study, an impact on the N uptake efficiency cannot completely be excluded. However, except genotype 1 in 2019, there was no genotypic difference in N uptake efficiency, pointing to a minor impact of the root system. If N uptake efficiency is enhanced by a superior root system, the genotype will be superior in particular under low N supply. Assuming that the genotypes are representative with sufficient differences, the lack of interaction between genotype and N supply suggests that there is no dominating genotypic effect of the root system regardless of N supply. All genotypes took up mineral nitrogen from soil with the same efficiency. Therefore, genotypic differences in NUE cannot be attributed to N uptake or N uptake efficiency but must originate from genotypic differences in N utilization efficiency.

4.3 N utilization efficiency (NUtE)

At the October harvest, the NUtE was in a similar range as observed for sugar and fodder beet grown under varying N supply at different sites (Laufer et al., 2016). Also for wheat, genotypic differences in NUtE and an interaction between genotype and N supply were observed (Gaju et al., 2011; Oliveira Silva et al., 2020). But in contrast to these studies with wheat, no interaction between genotype and N supply occurred in the current study with sugar beet.

A high NUtE can indicate an effective remobilization of N (Rathke et al., 2006). In this process, proteins are degraded, mostly RuBisCo at the beginning of senescence, and serve as N source (Masclaux-Daubresse et al., 2010). For *Arabidopsis*, the rate of N remobilization was positively correlated with the severity of leaf senescence, so that nitrogen was earlier available for remobilization in early senescing lines (Diaz et al., 2008). Increased remobilization also occurs during grain filling of cereals and oilseed rape (Cliquet et al., 1990; Malagoli et al., 2005; Masclaux-Daubresse et al., 2010). For sugar beet, N remobilization starts in early August with N being translocated from older to younger leaves and storage root tissue (Armstrong et al., 1986; Bürcky and Boscoe, 1983). The vegetative stage without bolting or flowering indicates for sugar beet an overall more constant and balanced remobilization. As sugar beet is in most growth stages sink, not source limited (Hoffmann et al., 2020; Hoffmann, 2019), an increased formation of new leaves is supposed to only slightly influence N utilization efficiency and sugar yield. A higher N remobilization from leaves to storage root tissue of individual genotypes would result in a significantly higher N uptake in the storage root. As no substantial genotypic differences in N uptake in leaves and root occurred, it can be assumed that all genotypes remobilized N with the same rates. Hence, genotypic differences in NUtE and thus NUE do not seem to result from differences in N uptake, but from differences in sugar yield.

4.4 Effect of assimilate partitioning and leaf N content on sugar yield

In the current study, the fraction of sugar to total dry matter was in a similar range as observed by Hoffmann (2019). Interestingly, genotypic variation in the fraction of sugar to total dry matter occurred. The genotype with the greatest proportion of sugar had the smallest proportion of leaf dry matter. This is in accordance with Hoffmann (2019) who concluded that the partitioning of assimilates between sugar storage and structural elements utilized for growth was most important for high yields. This is regulated by the sink strength, and genotypic differences in sink strength are suggested to cause genotypic differences in sugar yield (Evans, 1975; Ho, 1988; Marcelis, 1996; Wyse, 1979).

For sugar beet, the storage root represents the most important sink. High N supply mainly influences the rapid expansion of the leaf canopy (Malnou et al., 2006). Therefore, N fertilization would be expected to increase source strength of the leaf canopy, at the expense of sugar stored in the sink. It was thus surprising that the sugar yield increased with increasing leaf N content in both young and old leaves. However, it is not clear, whether the high N content in the leaves favored high sugar yields or whether it was just a coincidence. Malnou et al. (2008) observed an increase in leaf greenness due to high N content associated with N application but concluded that there was no increase in the radiation use efficiency, the efficiency of the crop to produce dry matter from intercepted radiation. Also in studies with corn, variable values in dark green color index suggested that factors other than leaf N content influence yield (Rorie et al., 2011). The results of the current study suggest that a high leaf N content is more likely the result of a concentration effect of genotypes with a small leaf canopy. Thus, a high N content in the leaf could be the consequence of an assimilate partitioning optimized for sugar yield. However, from these results it does not become clear whether a small leaf canopy necessarily results in a high N content and constitutes the prerequisite for high yields. Possibly the correlation of sugar yield with low leaf dry matter and high leaf N concentration is not necessarily the cause for enhanced sugar beet growth. This relationship should thus be verified on a larger genotype set.

5 Conclusions

The current study has shown that for sugar beet, genotypic differences in NUE result from genotypic differences in sugar yield potential. This follows from the lack of a relevant genotype by N supply interaction for NUE, so that genotypic differences arose independently of N supply. Genotypic differences in sugar yield were mainly caused by assimilate partitioning in favor of sugar storage, resulting in a high NUE. The selection for high sugar yield will therefore also lead to genotypes with high NUE. Furthermore, our results demonstrate that a high leaf mass is not a prerequisite for high sugar yield. Whether a high leaf N content (presumably resulting from the lower leaf mass) could be used to select for genotypes with their assimilate partitioning optimized for high sugar yield is questionable and cannot be clarified with these data. Further research with a broader range of different N supplies and a more detailed study of leaf N content is needed.

Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Epilog

Die Voraussetzung für hohe Erträge von Nutzpflanzen ist eine ausreichende Versorgung mit Wasser und Nährstoffen. Aufgrund klimatischer Veränderungen wird in Zukunft eine eingeschränkte Verfügbarkeit dieser Ressourcen erwartet. Um Ertragseinbußen zu vermeiden, werden Sorten benötigt, die eine hohe Effizienz in der Nutzung dieser Ressourcen haben und Wachstumsphasen mit eingeschränkter Ressourcenverfügbarkeit überstehen können. Im Folgenden wird daher der Zusammenhang von Wasserversorgung und Wachstum von Zuckerrüben dargestellt, um zu zeigen, in welcher Wachstumsphase der höchste Wasserbedarf besteht und die Ertragsbildung am stärksten beeinträchtigt wird. Des Weiteren sollen Ursachen für genotypische Variation in der Wasser- und Stickstoffnutzungseffizienz diskutiert werden. Dabei wird aufgezeigt, weshalb Genotypen nach Selektion auf ein hohes Zuckerertragspotential unter verschiedenen Umweltbedingungen überlegen sind. Diesbezüglich soll auch der Einfluss einer optimalen Assimilatverteilung als mögliche Ursache für genotypische Unterschiede im Zuckerertragspotential erörtert werden.

1 Reaktion auf Trockenstress

1.1 Wachstum und Wasserbedarf

Für die Entwicklung von Sorten mit spezieller Anpassung an bestimmte Umweltbedingungen bedarf es genotypischer Variation. In der Wachstumsphase, in der der Wasserbedarf am größten ist und entsprechend auch das Wachstum und die Ertragsbildung durch Trockenstress am stärksten beeinträchtigt werden, kann die größte genotypische Variation in der Reaktion auf Trockenstress erwartet werden.

Der Bedarf nach Ressourcen wie Wasser wird grundsätzlich von der Photosyntheseaktivität und somit vom Wachstum bestimmt (Körner 2013, 2015; Fatichi et al. 2014; White et al. 2016). Vor allem durch den Einfluss von Trockenstress ändern sich die Wachstumsraten. Um diese Änderungen während der Vegetationsperiode exakt zu untersuchen, gibt es verschiedene Möglichkeiten. Mit Hilfe von Sensortechnik zur Phänotypisierung kann das Wachstum zerstörungsfrei untersucht werden, wie bereits bei verschiedenen Fruchtarten gezeigt werden konnte (Tumilsa 2017; Hassan et al. 2019; Raeva et al. 2019; Feng et al.

2020; Tirado et al. 2020). Die Voraussetzung hierfür ist eine enge Beziehung zwischen der Höhe der absorbierten Strahlung und damit der Blattfläche und dem Ertrag, die für viele Kulturpflanzen besteht (Khurana und McLaren 1982; Board et al. 1992; Edwards et al. 2005). Bei Zuckerrüben wurde dagegen kein eindeutiger Zusammenhang zwischen der Blattfläche und dem Rüben- bzw. Zuckerertrag festgestellt (Clover et al. 2001; Hoffmann und Blomberg 2004; Hoffmann 2019), sodass andere Verfahren zur Erfassung von Wachstumsprozessen und Ertragsermittlung angewendet werden müssen. Ein solches Verfahren kann die regelmäßige Bestimmung des Rübendurchmessers sein, mit dem in den vorliegenden Versuchen (Manuskript I) das Wachstum von Zuckerrüben und die daraus ermittelten Wachstumsraten beschrieben wurde. Dies ist möglich, da bei Zuckerrüben der Rübendurchmesser in enger Beziehung zum Rübenertrag steht (Doney 1979; Hoffmann 2017). Dabei zeigte sich ein paralleler Verlauf von Wachstumsraten und Wasserverbrauch mit Maximum im Frühsommer. Das bestätigt, dass der Wasserbedarf von Zuckerrüben von den Wachstumsraten bestimmt wird. Da beide im Frühsommer am höchsten waren, ergibt sich für Zuckerrüben in dieser Wachstumsphase folglich die höchste Empfindlichkeit gegenüber Trockenstress. Daher hat, wie bereits bei Brown et al. (1987) beobachtet, früher Trockenstress stärkere Auswirkungen als Trockenstress in einer späteren Wachstumsphase. Der Rübendurchmesser von Zuckerrüben, die einer Trockenstressperiode ausgesetzt waren, entwickelt sich nach dem Trockenstressereignis nahezu parallel zu ungestressten Zuckerrübenpflanzen. Dies deutet darauf hin, dass die Ertragsminderung durch Trockenstress im Laufe des Wachstums nicht mehr kompensiert werden kann. Weiterhin ist es ein Anzeichen dafür, dass es bei Zuckerrüben nach Trockenstress keine dauerhafte Beeinträchtigung des Wachstums oder der Ertragsbildung gibt. Bei anderen Fruchtarten wie Getreide oder Mais kann Trockenstress gerade während Wachstumsphasen wie Schossen, Blüte oder Kornfüllung das Wachstum und die Ertragsbildung tiefgreifend beeinträchtigen (Barnabás et al. 2008). Zuckerrüben hingegen werden noch während des vegetativen Wachstums geerntet, sodass keine für Trockenstress besonders anfälligen Wachstumsphasen wie Schossen oder Blüte auftreten (Dunham 1993).

Handlungsempfehlungen für den Zuckerrübenanbau in der landwirtschaftlichen Praxis können aus diesen Erkenntnissen für Standorte mit der Möglichkeit zur Bewässerung abgeleitet werden. Eine Bewässerung sollte am ehesten im Frühsommer, in der Phase mit dem höchsten Wasserbedarf, eingesetzt werden. Da es keine Anzeichen für eine Kompensation der Beeinträchtigungen durch Trockenstress gibt, scheint der Nutzen von Wassergaben in späteren Wachstumsphase begrenzt zu sein, vor allem wegen der geringeren

Wachstumsraten in späteren Wachstumsphasen. Späte Wassergaben führen zwar zu einer Erhöhung des Rübenertrages, weil die Zellen im Rübenkörper mit Wasser gefüllt werden. Gleichzeitig wird aber der Zuckergehalt verdünnt, sodass es keine nennenswerte Steigerung des Zuckerertrages gibt. Auch für die Abschätzung der Erntemengen in den Zuckerfabriken können diese Erkenntnisse hilfreich sein. Da bei Trockenstress in späteren Wachstumsphasen die Ertragsbildung nicht so stark beeinträchtigt wird wie in früheren Wachstumsphasen, ist nur mit geringen Abweichungen von der getroffenen Ernteprognose zu rechnen.

1.2 Trockenstresstoleranz

Eine spezielle Anpassung an Bedingungen mit Trockenstress würde voraussetzen, dass es eine Interaktion zwischen Genotyp und Wasserangebot gibt. Da die Trockenstressempfindlichkeit in einer frühen Wachstumsphase am größten ist, kann in dieser Phase auch die größte genotypische Variation in der Reaktion auf Trockenstress erwartet werden. Als erstes werden die Auswirkungen von Trockenstress durch Welken der Blätter sichtbar. Daher konnte genotypische Variation in der Reaktion auf Trockenstress bisher vor allem in Blattmerkmalen beobachtet werden und weniger in Merkmalen mit engem Bezug zur Ertragsbildung (Ober und Luterbacher 2002; Ober et al. 2005). Es ist fraglich, ob diese Welkereaktion der Blätter relevant für die späteren Ertragseinbußen ist und somit für die Bewertung der Trockentoleranz von Genotypen hilfreich sein kann. Ebenso deuten die positive Beziehung zwischen Zuckererträgen mit und ohne Bewässerung (Ober et al. 2004) sowie die fehlende Interaktion zwischen Genotyp und Wasserversorgung bei der Wassernutzungseffizienz (WNE) (Bloch et al. 2006b) bereits darauf hin, dass bei Zuckerrüben eine spezielle Anpassung an Trockenstressbedingungen nicht auftritt oder zumindest sehr schwierig festzustellen ist.

Auch in der vorliegenden Arbeit gab es weder für die WNE in den Gewächshausversuchen (Manuskript I) noch bei weitgehender Kontrolle von Krankheiten für den Zuckerertrag in den Feldversuchen (Manuskript II) eine relevante Interaktion zwischen Genotyp und Wasserversorgung. Das bedeutet, dass die Genotypen, die bei ausreichender Wasserversorgung überlegen sind, auch bei Trockenstress überlegen sind. Somit gibt es bei Zuckerrüben keine spezielle Anpassung an Trockenstressbedingungen und daher keine vom Genotyp abhängige Trockenstresstoleranz. Die Ergebnisse lassen darauf schließen, dass genotypische Unterschiede in der WNE unabhängig vom Wasserangebot entstehen und somit die Folge von Unterschieden im Zuckerertragspotential sind. Daher hatte der Genotyp mit dem höchsten Zuckerertragspotential auch die höchste WNE, sowohl bei Trockenstress als auch bei ausreichender Wasserversorgung.

2 Reaktion auf unterschiedliches Stickstoffangebot

2.1 Stickstoffnutzungseffizienz

Bei Zuckerrüben beschreibt die Stickstoffnutzungseffizienz (SNE) den Zuckerertrag, der mit einer Einheit des im Boden verfügbaren Stickstoffs gebildet werden kann (Moll et al. 1982). In den vorliegenden Versuchen (Manuskript III) wurde gezeigt, dass wie bei der WNE auch bei der SNE keine relevante Interaktion zwischen den Genotypen und dem Stickstoffangebot aufgetreten ist. Das bedeutet, dass die genotypische Variation in der SNE bei Zuckerrüben, ähnlich zur WNE, unabhängig vom Stickstoffangebot ist und damit auf Unterschieden im Zuckerertragspotential beruht. Diese geringe Variation kann darauf zurückgeführt werden, dass bei Zuckerrüben das Haupternteprodukt Zucker ist, welches keinen Stickstoff enthält (Hoffmann et al. 2005). Dadurch gibt es für die Zuckerspeicherung keine Phasen mit besonders hohem Stickstoffbedarf (lediglich für die Blattbildung ist der Stickstoffbedarf im Frühjahr erhöht), auf die die Genotypen unterschiedlich reagieren könnten. Eine unterschiedliche Reaktion hätte Auswirkungen auf den genotypischen Zuckerertrag und damit auch Einfluss auf die genotypische SNE.

2.2 Assimilatverteilung

Größeren Einfluss auf das Zuckerertragspotential und damit auf die Effizienz in der Nutzung der eingesetzten Ressourcen Stickstoff, aber auch Wasser, scheint eine optimale Verteilung der Assimilate in der Pflanze zu haben. Das Stickstoffangebot fördert bei Zuckerrüben in erster Linie die Blattbildung, weniger die Ertragsbildung (Malnou et al. 2006, 2008). Eine große Blattfläche ist bei Zuckerrüben aber keine zwingende Voraussetzung für hohe Erträge, da Wachstum und Ertragsbildung nur in einer kurzen Periode während der Vegetationszeit von der Assimilatproduktion in den Blättern (Source), meistens aber von der Kapazität der Assimilateinlagerung (Sink) limitiert werden (Hoffmann 2019; Hoffmann et al. 2020). Die optimale Verteilung der Assimilate entweder zur Bildung von Strukturelementen zum Wachstum oder für die Zuckereinlagerung in der Rübe sind entscheidend für hohe Erträge

(Hoffmann 2019). Auch in den vorliegenden Versuchen (Manuskript III) wurden genotypische Unterschiede in der Aufteilung der Gesamttrockenmasse beobachtet. Dabei hatten die Genotypen mit einem geringerem Anteil Blatt einen größeren Anteil Zucker an der Gesamttrockenmasse und damit höhere Zuckererträge, was zu einer höheren SNE führte. Diese Genotypen erzielten unabhängig von der Wasserversorgung höhere Zuckererträge und wiesen folglich auch eine höhere WNE auf (Manuskript I und II).

Eine schnelle Jugendentwicklung mit frühzeitig geschlossenem Blattapparat ermöglicht bereits im Frühjahr eine hohe Strahlungsabsorption und ist somit wichtig für das Erzielen hoher Zuckererträge (Jaggard et al. 2009b; Hoffmann und Kluge-Severin 2010). Zudem kann eine vollständige Bodenbedeckung durch den Blattapparat bei Zuckerrüben Vorteile bei der Unkrautunterdrückung oder der Verminderung von Evaporation haben (Turner 2004; Jursík et al. 2008). Dennoch zeigt die vorliegende Arbeit, dass bei Zuckerrüben eine große Blattfläche im Sommer nicht die Voraussetzung für hohe Zuckererträge ist. Es wird vielmehr deutlich, dass von der Blattfläche keine verlässlichen Rückschlüsse auf den Zuckerertrag gezogen werden können. Eine enge Beziehung zwischen der Blattfläche und dem Zuckerertrag würde es ermöglichen, durch Phänotypisierung genotypische Unterschiede im Wachstum und der Ertragsbildung zu identifizieren. Dies ist bei anderen Fruchtarten möglich und würde auch bei Zuckerrüben die nicht-destruktive Merkmalserfassung in Forschung und Züchtung vereinfachen (Raeva et al. 2019; Tirado et al. 2020). Ebenso ist es für die Zuckerfabriken für die Kampagnenplanung von Bedeutung, die Ertragsmenge vor der Ernte möglichst genau und mit einfachen Mittel abschätzen zu können. Dazu werden bisher Proberodungen durchgeführt, um eine Prognose über die Erntemenge zu erstellen (Krumbiegel 1968). Die Ergebnisse der vorliegenden Arbeit lassen bezweifeln, dass mittels optischer Verfahren der Phänotypisierung über Blatteigenschaften verlässliche Rückschlüsse auf die Höhe der Erträge oder Ertragsunterschiede zwischen Genotypen gezogen werden können.

3 Züchtung von Sorten mit hoher Ressourceneffizienz

3.1 Selektion auf Zuckerertragspotential

Die Ergebnisse der vorliegenden Arbeit haben gezeigt, dass genotypische Unterschiede in der WNE und der SNE maßgeblich von Unterschieden im Zuckerertragspotential bestimmt werden. Dies kann bei weitgehender Kontrolle von Krankheiten somit als relevantes

Merkmal für die Selektion von Genotypen mit Anpassung an variable Wasser- oder Stickstoffversorgung und hoher Ressourceneffizienz gesehen werden. Dabei macht es keinen Unterschied, ob unter optimaler oder begrenzter Verfügbarkeit dieser Ressourcen selektiert wird, weil der Genotyp mit dem höchsten Zuckerertrag unter allen Bedingungen überlegen ist. Für die Selektion von Genotypen mit hoher WNE ist dies jedoch etwas differenzierter zu betrachten, da sich der Zuckerertrag aus Rübenertrag und Zuckergehalt zusammensetzt und diese Parameter auf Trockenstress unterschiedlich reagieren.

Bei Trockenheit wird der Wassergehalt in den Zellen des Rübenkörpers reduziert. Dadurch sinkt zwar der Rübenertrag, der Zucker wird aber gleichzeitig aufkonzentriert (Bloch et al. 2006a; Milford 2006). Daher sind bei Trockenstress die Zuckergehalte höher, während bei ausreichender Wasserversorgung höhere Rübenerträge erzielt werden (Artschwager 1926; Milford 1973; Doney et al. 1981; Allison et al. 1996). Folglich wird ein geringerer Rübenertrag durch einen höheren Zuckergehalt zumindest partiell kompensiert, sodass aus dem offensichtlichen Rückgang des Rübenertrags als Reaktion auf Trockenstress keine endgültigen Rückschlüsse auf die Höhe des Zuckerertrages gezogen werden können.

In den vorliegenden Versuchen (Manuskript II) wurde diese gegensätzliche Beziehung zwischen Rübenertrag und Zuckergehalt bei Zuckererträgen zwischen 10 und 20 t ha^{-1} bestätigt. Wenn berücksichtigt wird, dass die Zuckererträge in Parzellenversuchen im Vergleich zum Anbau in der Praxis etwas höher sind (Laidig et al. 2014), kann das Ertragsspektrum aus diesen Versuchen einen großen Teil der Zuckerrübenanbaufläche in den wichtigsten Anbauländern Europas widerspiegeln (Bruhns und Mosolff 2020; Statista 2021). Dabei traten die größten genotypischen Unterschiede sowohl im Zuckergehalt als auch im Rübenertrag bei ausreichender Wasserversorgung auf. Daher wird die Selektion bei ausreichender Wasserversorgung immer die besten Genotypen hervorbringen, unabhängig davon, unter welchen Bedingungen später der Anbau stattfindet. Zudem lassen sich unter diesen Bedingungen die Genotypen auch eindeutig als E- oder Z-Typen (Typen mit hohem Rübenertrag oder Zuckergehalt) (Bosemark 1993) klassifizieren. Die Selektion unter optimalen Bedingungen bietet für die Züchtung den Vorteil, dass die Anzahl an Testumwelten reduziert werden kann, weil keine speziellen Trockenstressumwelten für die Selektion benötigt werden. Dies ist auch dahingehend von Vorteil, weil verlässlicher Trockenstress im Feld lediglich mit Hilfe von Rain Sheltern simuliert werden kann. Dabei ist die Installation sehr aufwendig, die Versuchsfläche begrenzt und außerdem können Unterschiede in der Luft- und Bodentemperatur innerhalb der Rain Shelter im Vergleich zum Freiland entstehen (Brown et al. 1987; Yahdjian und Sala 2002). Für den Anbau ist von

Vorteil, dass der Genotyp nicht in Abhängigkeit vom möglichen Auftreten von Trockenstress ausgewählt werden muss, was vor dem Hintergrund wechselnder und nicht vorhersagbarer Jahreswitterung unmöglich erscheint.

3.2 Einfluss von Krankheiten auf das Genotypenranking

Eine spezielle Anpassung an bestimmte Umweltbedingungen wie Trockenstress oder begrenztes Stickstoffangebot setzt eine Interaktion zwischen Genotyp und Umwelt voraus. Diese tritt z. B. bei Mais, Getreide und Soja auf (Patterson et al. 1977; Weber und Westermann 1994; Ribaut et al. 1996; 1997; Cucolotto et al. 2007; Yan et al. 2010), sodass es bei diesen Fruchtarten spezielle Anpassungen an bestimmte Umweltbedingungen gibt und sich das Genotypenranking in den unterschiedlichen Umwelten ändert. Bei voller agronomischer Intensität und damit weitgehender Kontrolle von Krankheiten und Schädlingen wurde jedoch in Versuchen von Voss-Fels et al. (2019) auch zwischen bewässerten und unbewässerten Varianten in den Weizenerträgen eine enge Korrelation beobachtet. Dies deutet darauf hin, dass auch bei Getreide in der Abwesenheit von Krankheiten keine Genotyp-Umwelt Interaktion auftritt. Bei Zuckerrüben wurde durch Krankheitsbefall eine Änderung im Genotypenranking beschrieben, die somit das Auftreten von Interaktionen erklärt (Märländer et al. 2018; Laufer et al. 2020). In den vorliegenden Versuchen (Manuskript I, II, III) wurde keine relevante Interaktion beobachtet, weil das Auftreten von Krankheiten verhindert wurde. Folglich kann daraus geschlossen werden, dass Genotyp-Umwelt-Interaktionen wahrscheinlich durch genotypische Unterschiede im Resistenzniveau gegenüber Krankheiten, aber nicht in der Ertragsreaktion entstehen.

Der Zusammenhang zwischen Resistenzniveau, Witterung und Genotypenranking kann am Beispiel der Blattfleckenkrankheit *Cercospora beticola* Sacc. aufgezeigt werden. Diese Krankheit kann sich optimal bei trocken-warmer Witterung mit gelegentlichen Niederschlägen oder hoher Luftfeuchtigkeit entwickeln (Windels et al. 1998), weshalb ein stärkerer Befall in Jahren mit ausreichenden Niederschlägen oder unter Bewässerung zu beobachten ist (Paulus et al. 1971; Pundhir und Mukhopadhyay 1987). Somit stellt Trockenstress für diese Krankheit eine ungünstige Bedingung dar. Aufgrund unterschiedlicher Resistenzniveaus gegenüber *Cercospora beticola* können Unterschiede im Genotypenranking bei ausreichender Wasserversorgung im Vergleich zu Trockenstressbedingungen entstehen. Diese Unterschiede beruhen aber auf Interaktionen der Genotypen mit dem Krankheitsbefall und nicht auf einer Trockentoleranz. Dies kann zu Fehlinterpretationen in der Bewertung von Sorteneigenschaften führen.

Es kann ebenso vorkommen, dass sich das Genotypenranking in der SNE oder der WNE unter ökologischen und konventionellen Anbaubedingungen unterscheidet. Die Möglichkeiten zum Pflanzenschutz sind in der ökologischen Landwirtschaft begrenzt (Speiser und Tamm 2011). Bei Zuckerrüben kann z. B. eine stärkere Unkrautkonkurrenz die Pflanzenentwicklung stören oder das Auftreten von Krankheiten wie Wurzelbrand als Folge eingeschränkter Beizmöglichkeiten die Pflanzendichte reduzieren (Duffus und Ruppel 1993). Daraus resultieren Beeinträchtigungen in der Zuckerertragsbildung. Auch wenn es keine direkte Beziehung zwischen Blattfläche und Zuckerertrag gibt, können genotypische Unterschiede in Blatteigenschaften oder dem Jugendwachstum, die der Bodenbedeckung dienen, indirekten Einfluss auf den Zuckerertrag haben. Durch die entstehenden Unterschiede in der Unkrautunterdrückung oder der Verminderung von Evaporation kann das Genotypenranking im Zuckerertrag verändert werden, ebenso wie durch Unterschiede in der Anfälligkeit von Krankheiten. Unter konventionellen Bedingungen gibt es mehr Möglichkeiten den Krankheits- und Unkrautdruck zu kontrollieren, sodass die Interaktion zwischen Genotyp und Umwelt wahrscheinlich geringer ist als im ökologischen Anbau. Dadurch wird der Einfluss auf das Genotypenranking im Zuckerertrag vermindert. Da das Zuckerertragspotential die SNE und die WNE bestimmt, können mögliche genotypische Unterschiede in der Ressourceneffizienz unter konventionellen im Vergleich zu ökologischen Bedingungen erklärt werden. Dies kann als Interaktion zwischen Genotyp und Anbausystem bezeichnet werden (Francis und Smith 1985; Gebeyehu et al. 2006; Murphy et al. 2007).

4 Ausblick

In Zukunft werden höhere Temperaturen und häufigere Perioden mit Trockenheit erwartet. Zuckerrüben können die Auswirkungen dieser abiotischen Stressfaktoren im Vergleich zu anderen Fruchtarten gut überstehen (Dunham 1993; Ober und Rajabi 2010). Dennoch gilt Trockenstress auch bei Zuckerrüben als bedeutender ertragsbegrenzender Faktor und beeinträchtigt die Verarbeitungsqualität (Pidgeon et al. 2001; Bloch und Hoffmann 2005; Bloch et al. 2006a; Lipiec et al. 2013). Eine Zunahme in der Variabilität der Witterungsbedingungen wird aufgrund des Klimawandels erwartet (Rummukainen 2012), sodass auch bei Zuckerrüben mit stärkeren Ertragsschwankungen gerechnet werden muss.

Die vorliegende Arbeit hat gezeigt, dass es bei Zuckerrüben keine genotypischen Anpassungen an abiotische Umweltfaktoren und daher auch keine Genotypen mit Trockenstresstoleranz gibt. Vielmehr sind Genotypen mit hohem Zuckerertrag bei unterschiedlichen Umweltbedingungen überlegen und damit auch effizient in der Nutzung anderer Ressourcen. Ebenso ist auch ein Temperaturanstieg im Frühjahr eher positiv für den Zuckerrübenanbau zu bewerten (im Gegensatz zum Sommer), weil sich dadurch die Vegetationszeit verlängern kann. Ein früherer Vegetationsbeginn mit einem geringeren Risiko für Spätfröste hat dabei positiven Einfluss auf die Ertragsbildung (Jones et al. 2003).

Als Folge dieser klimatischen Veränderungen mit Trockenheit und höheren Temperaturen entwickeln sich jedoch auch optimale Lebensbedingungen für Krankheiten und Schädlinge, sodass die Zunahme vorhandener oder die Entstehung neuer biotischer Stressfaktoren erwartet werden kann. Modellrechnungen belegen, dass in Zukunft ein früheres und stärkeres Auftreten der Blattfleckenkrankheit *Cercospora beticola* zu erwarten ist (Kremer et al. 2016). Bei der Schilf-Glasflügelzikade (*Pentastiridius leporinus* L.) handelt es sich um einen neuen biotischen Stressfaktor, der aufgrund steigender Temperaturen sein Verbreitungsgebiet erweitert hat und daher mittlerweile auch in bestimmten Teilen von Deutschland auftritt (Pfitzer et al. 2020). Probleme für den Zuckerrübenanbau entstehen durch die Übertragung von pflanzenpathogenen Bakterien, die die Krankheit SBR (Syndrome Basses Richesses) auslösen. Die Folge sind Zuckerrübenpflanzen mit geringen Zuckergehalten und teils massiven Ertragseinbußen (Bressan et al. 2008). Bei steigenden Temperaturen können möglicherweise mehrere Generationszyklen der Schilf-Glasflügelzikade im Jahr durchlaufen werden. Damit ist eine Ausdehnung des Befallsgebiets und somit eine Verschärfung dieser Problematik durch den Klimawandel zu erwarten (Pfitzer et al. 2020). Höhere Temperaturen in Kombination mit Phasen von Trockenheit verbessern auch die Lebensbedingungen der Rübenmotte (Berker und Löcher 1959; Rieckmann und Steck 1995). Mehrere Generationen von Larven können sich etablieren, deren Fraßschäden Eintrittspforten für Fäulniserreger am Rübenkörper darstellen (Löcher 1960). Darüber hinaus erschweren veränderte Rahmenbedingungen bezüglich des Pflanzenschutzmitteleinsatzes die Bekämpfung von Blattläusen, die als Virusvektoren fungieren. Dadurch steigt das Risiko eines Befalls mit der virösen Vergilbung, die erhebliche Ertragseinbußen verursachen kann (Hossain et al. 2019; Hossain et al. 2021).

Genotypische Unterschiede in der Anfälligkeit gegenüber diesen biotischen Faktoren können die Rangfolge von Sorten in unterschiedlichen Umwelten verändern. Daher ist die

Resistenz- und Toleranzzüchtung wichtig, um Sorten mit einer geringen Anfälligkeit gegenüber Krankheiten und Schädlingen zu entwickeln. Neben der Züchtung gibt es auch neuere Forschungsansätze, um mit Hilfe ackerbaulicher Maßnahmen den Einfluss biotischer Faktoren zu reduzieren. So sollen durch die Anlage von Blühstreifen gezielt Lebensräume für schädlingsreduzierende Nützlinge bereitgestellt werden, die in den angrenzenden Feldern die Schädlingspopulation reduzieren (Albrecht et al. 2020). In Versuchen mit Kartoffeln konnte dadurch eine Reduktion der Anzahl an Blattläusen erzielt werden (Tschumi et al. 2016). Inwiefern diese Maßnahmen auch bei Zuckerrüben eine effektive Wirkung erzielen, wird in aktuellen Versuchen untersucht (BLE 2021).

Wenn durch züchterische und ackerbauliche Maßnahmen der Einfluss der biotischen Stressfaktoren reduziert werden kann, können Sorten ihr Zuckerertragspotential voll ausschöpfen und die Interaktion zwischen Sorte und Umwelt ist gering. Dadurch sind Sorten stabil in verschiedenen Umwelten, sodass die Sorten mit dem höchsten Zuckerertrag bei ausreichender Wasserversorgung auch unter Trockenstressbedingungen überlegen sind. Durch ein hohes Zuckerertragspotential wird somit eine hohe WNE und SNE erzielt und insgesamt die Ressourceneffizienz verbessert.

Zusammenfassung

Natürliche Ressourcen wie Wasser und Stickstoff sind unverzichtbar für das Pflanzenwachstum. Die Wasserverfügbarkeit wird jedoch in Zukunft aufgrund klimatischer Veränderungen häufiger begrenzt sein, sodass auch bei Zuckerrüben Sorten benötigt werden, die Trockenstressphasen überdauern können und effizient in der Wassernutzung sind. Auch ein effizienter und nachhaltiger Einsatz von Stickstoff ist anzustreben, da zu hohe Stickstoffmengen mit umweltschädlichen Emissionen einhergehen. Um mögliche Ansatzpunkte für die züchterische Verbesserung der Ressourceneffizienz von Zuckerrüben zu erlangen, sollte im ersten Teil dieser Arbeit der Effekt von Trockenstress und im zweiten Teil die Reaktion auf ein unterschiedliches Stickstoffangebot bei verschiedenen Zuckerrübengenotypen untersucht werden.

Für die Entwicklung trockentoleranter Zuckerrübensorten ist es wichtig, die Wachstumsphase mit der stärksten Reaktion auf Trockenstress zu kennen, damit in dieser Phase gezielt selektiert werden kann. Ebenso sollte es nach Möglichkeit ein Merkmal geben, mit dem an Trockenstress-bedingungen angepasste Genotypen identifiziert werden können. Daher wurde in den in Manuskript I beschriebenen Versuchen untersucht, in welcher Wachstumsphase Zuckerrüben den höchsten Wasserbedarf haben und folglich am anfälligsten für Trockenstress sind. Außerdem sollte Ursachen für genotypische Unterschiede in der Wassernutzungseffizienz (WNE) nachgegangen sowie geprüft werden, ob das Merkmal WNE zur Selektion von Genotypen mit Anpassung an Trockenstress geeignet ist. Dafür wurden in den Jahren 2019 und 2020 im Gewächshaus Gefäßversuche mit vier Genotypen durchgeführt. Durch eine Reduktion der Bewässerung auf 50 % der Wasserhaltekapazität (WHK) wurde eine vierwöchige Trockenstressperiode in unterschiedlichen Wachstumsphasen simuliert. Bei unbegrenzter Wasserversorgung (100 % WHK) entwickelte sich der Wasserverbrauch parallel zur Wachstumsrate der Rübe. Dies deutet darauf hin, dass der Wasserbedarf durch die Wachstumsrate bestimmt wird. Daher verursachte früher Trockenstress in der Phase mit der höchsten Wachstumsrate die stärkste Ertragsminderung, die später in der Vegetationsperiode nicht mehr kompensiert werden konnte. Im Gegensatz zum Zuckerertrag unterschied sich der Wasserverbrauch zwischen den Genotypen, was zu genotypischen Unterschieden in der WNE führte. Dabei trat jedoch keine relevante Interaktion zwischen Genotyp und Wasserversorgung auf, sodass es keinen Hinweis auf eine Trockentoleranz der Genotypen mit hoher WNE gab. Vielmehr

deuten die Ergebnisse darauf hin, dass die WNE eher durch das Zuckerertragspotenzial eines Genotyps als durch die Wasserversorgung bestimmt wird. Daher sollte bei der Züchtung von Zuckerrübengenotypen mit Anpassung an Umwelten mit wechselnder Wasserversorgung nach dem Zuckerertragspotenzial selektiert werden.

Manuskript II zielte darauf ab, unter natürlichen Bedingungen Ursachen für genotypische Unterschiede in der Reaktion auf verschiedene Umwelteinflüsse, insbesondere Trockenstress, zu untersuchen. Dabei sollten Umweltbedingungen definiert werden, unter denen Zuckerrüben am besten selektiert werden können, um diese hinsichtlich Rübenertrag und Zuckergehalt klassifizieren zu können. Ferner sollte der Zusammenhang zwischen Ertragspotenzial und Ertragsstabilität analysiert werden. Dazu wurde in Feldversuchen in den Jahren 2018 und 2019 an drei Standorten in Italien, Frankreich und Deutschland die Reaktion von sechs Genotypen auf Trockenstress untersucht, wobei eine Bewässerungsvariante den Vergleich mit optimalen Wachstumsbedingungen ermöglichte. Ferner wurden Versuche an einem weiteren Standort mit drei unterschiedlichen Stickstoffangebotsstufen einbezogen. In der Abwesenheit von Krankheiten konnten keine signifikanten Unterschiede zwischen den Genotypen in der Reaktion des Zuckerertrags auf unterschiedliches Wasser- und Stickstoffangebot beobachtet werden (keine Genotyp-Umwelt-Interaktion). Somit lieferten die Versuche keinen Hinweis auf Genotypen mit einer besonderen Anpassung an Trockenstressbedingungen. Dies ist wahrscheinlich auf eine Limitierung der Zuckerspeicherung durch die Senke (Sink) zurückzuführen. Für den Zuckergehalt und den Rübenertrag bestand dagegen eine Genotyp-Umwelt-Interaktion. Bei beiden Merkmalen zeigten sich die größten genotypischen Unterschiede bei ausreichender Wasserversorgung. Daher kann die Klassifizierung von Genotypen nach hohem Rübenertrag oder hohem Zuckergehalt am genauesten unter optimalen Wachstumsbedingungen erfolgen. Beim Zuckerertrag traten genotypische Unterschiede im Ertragspotenzial und der Ertragsstabilität auf. Jedoch war ein hohes Ertragspotenzial nicht unbedingt mit einer hohen Ertragsstabilität verbunden. Da es wichtig ist, auch bei höherer Variabilität der klimatischen Bedingungen konstant hohe Erträge zu erzielen, wird die Ertragsstabilität zukünftig in der Züchtung an Bedeutung gewinnen.

Neben einer effizienten Wassernutzung ist auch die effiziente Verwendung von Ressourcen wie Stickstoff wichtig für eine nachhaltige Pflanzenproduktion. Daher wurden in Manuskript III die Gründe für eine genotypische Variation in der Stickstoffnutzungseffizienz (SNE) von unterschiedlichen Zuckerrübengenotypen untersucht und diskutiert. In den Jahren 2018 und 2019 wurden sechs Genotypen in Feldversuchen bei unterschiedlichen Stickstoffangebotsstufen mit 65, 120 und 240 kg N ha^{-1} untersucht. Die Versuche zeigten nur geringe genotypische Unterschiede in der N Aufnahme und der N-Aufnahmeeffizienz. Dagegen traten deutliche genotypische Unterschiede in der SNE auf. Die vernachlässigbare Interaktion zwischen Genotyp und Umwelt deutet darauf hin, dass die Unterschiede in der SNE unabhängig von der N Versorgung aufgetreten sind und dass es keine Genotypen mit spezieller Anpassung an Bedingungen mit geringer N Verfügbarkeit gab. Vielmehr resultierten die Unterschiede in der SNE aus Unterschieden im Zuckerertragspotenzial, sodass eine Selektion auf ein hohes Zuckerertragspotenzial auch zu Genotypen mit hoher SNE führt. Weiterhin konnte gefolgert werden, dass ein hohes Zuckerertragspotenzial aus einer günstigen Assimilatverteilung hin zu hohem Zuckerertrag mit einem geringen Anteil Blattmasse an der Gesamttrockenmasse resultierte. Dabei war eine geringere Blattmasse tendenziell mit einem höheren Blatt N Gehalt verbunden. Ob ein hoher N Gehalt im Blatt auch zur Identifizierung von ertragreichen Genotypen genutzt werden kann, ist unklar. Es konnte lediglich abgeleitet werden, dass eine hohe Blattmasse keine Voraussetzung für hohe Zuckererträge ist.

Die vorliegenden Ergebnisse deuten darauf hin, dass es keine Zuckerrübengenotypen mit einer speziellen Anpassung an Trockenstressbedingungen gibt. Da der Wasserbedarf von Zuckerrüben von der Wachstumsrate bestimmt wird, ist die Anfälligkeit für Trockenstress im Frühsommer, in der Phase mit den höchsten Wachstumsraten, am größten. Sowohl die Wassernutzungseffizienz als auch die Stickstoffnutzungseffizienz werden vom Zuckerertragspotential bestimmt, sodass bei der Entwicklung von Sorten für unterschiedliche Umweltbedingungen auf ein hohes Zuckerertragspotential selektiert werden sollte.

Summary

Natural resources such as water and nitrogen are essential for plant growth. In the future, water will be limited more frequently due to climatic changes. Therefore, also for sugar beet varieties are needed that can tolerate periods of drought stress and use water efficiently. The use of nitrogen should also be efficient and sustainable, as excessive amounts of nitrogen are associated with emissions that are harmful to the environment. In order to obtain approaches for breeding improvement of sugar beet resource efficiency, genotypic differences in response to drought stress were studied in the first part of this work. In the second part, the response to varying nitrogen supply of different sugar beet genotypes was investigated.

For the development of drought-adapted sugar beet varieties, it is important to know the growth period with the strongest reaction to drought stress and a trait that can be used to identify genotypes adapted to drought stress conditions. Therefore, the trials described in manuscript I investigated the growth period of sugar beet with highest water demand and consequently the highest susceptibility to drought stress. Furthermore, possible reasons for genotypic differences in water use efficiency (WUE) were investigated, and also if the trait WUE might be used for the selection of drought-adapted genotypes. For this purpose, pot experiments were conducted in the greenhouse with four genotypes in 2019 and 2020. Drought stress was simulated in different growth periods by reduction of irrigation to 50% of the water holding capacity (WHC) for four weeks. Under unlimited water supply (100% WHC), water consumption developed in parallel with the growth rate of the storage root. This indicates that water demand is determined by the growth rate. Therefore, early drought stress caused the most severe yield impairment in the period with the highest growth rate, which could not be compensated later in the season. In contrast to sugar yield, water use and thus WUE differed among genotypes. However, no relevant interaction between genotype and water supply occurred, so there was no evidence of drought tolerance among genotypes with high WUE. The results suggest that WUE is rather determined by the genotypic sugar yield potential than by water supply. When breeding sugar beet genotypes adapted to environments with variable water supply, selection should focus on high sugar yield potential.

Manuscript II summarizes trials which investigated reasons for genotypic differences in the response to different environments, in particular drought stress under natural conditions. In

addition, environmental conditions were defined for optimal selection for root yield and sugar content and the relationship between yield potential and yield stability was investigated. In 2018 and 2019, field trials were conducted with six genotypes at three sites in Italy, France and Germany with natural occurrence of drought. An irrigation treatment allowed the comparison with optimal growing conditions. Trials were also conducted with three different levels of nitrogen supply. In the absence of disease, no significant differences in the sugar yield response to different water and nitrogen supply were observed between the genotypes (no genotype- environment interaction). Thus, the trials did not provide evidence for a particular adaptation of the genotypes to drought stress conditions, probably due to a limitation of sugar storage by the sink. In contrast, there was a genotype-environment interaction for sugar content and root yield. For both traits, the greatest genotypic differences occurred under sufficient water supply. Therefore, classification of genotypes by either high root yield or high sugar content can be carried out most accurately under optimal growth conditions. For sugar yield, genotypic differences occurred in yield potential and yield stability. High yield potential was not necessarily associated with high yield stability. As it is important to achieve consistently high yields even under higher variability of climatic conditions, yield stability will become more important in future breeding.

In addition to a high water use efficiency, the efficient use of other resources such as nitrogen is also important for efficient and sustainable crop production. Therefore, the reasons for genotypic variation in nitrogen use efficiency (NUE) of different sugar beet genotypes were investigated and discussed in manuscript III. In 2018 and 2019, six genotypes were evaluated in field trials under different N supply at 65, 120, and 240 kg N ha^{-1}. The trials showed only minor genotypic differences in N uptake and N uptake efficiency, but significant genotypic differences in NUE. The negligible interaction between genotype and environment suggests that the differences in NUE were independent of N supply and that there is no genotypic adaptation to low N availability. Rather, the differences in NUE resulted from differences in sugar yield potential. This indicates that selection for high sugar yield potential also rises NUE. Furthermore, it was concluded that high sugar yield potential results from a favorable assimilate partitioning towards high sugar yield with a low fraction of leaf mass to total dry mass. In consequence, there were indications that lower leaf mass was associated with higher leaf N content. Whether high leaf N content can be used to identify genotypes with high sugar yield potential is unclear, but it became evident that high leaf mass is not a prerequisite for high sugar yields.

The current results indicate that there are no sugar beet genotypes with special adaptions to drought stress conditions. As the water requirement of sugar beet is determined by the growth rate, the susceptibility to drought stress is highest in early summer, the period with the highest growth rates. Both water use efficiency and nitrogen use efficiency are determined by sugar yield potential, so selection should be made for high sugar yield potential when developing varieties superior under different environmental conditions.

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Veröffentlichungen und Vorträge während der Promotion

1 Veröffentlichte Manuskripte

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3 Tagungsbeiträge (Tagungsband)

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4 Vorträge

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Ebmeyer, H. (2021): Einfluss von Trockenstress auf Wasserverbrauch und Wachstum von Zuckerrüben. Online-Sitzung des Arbeitskreises Pflanzenbau des Instituts für Zuckerrübenforschung, 06.07.2021.

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