

附件 2

教学成果应用及效果证明材料

目录

1. 成果评定书（鉴定意见）	1
2. 相关证书.....	5
第七届中国国际“互联网+”大学生创新创业大赛证书（金奖）	5
优秀创新创业导师证书	6
第十二届全国大学生“挑战杯”竞赛证书（铜奖）	7
第七届云南省“互联网+”大学生创新创业大赛证书（金奖）	8
第六届云南省“互联网+”大学生创新创业大赛证书（银奖）	9
第六届云南省“互联网+”大学生创新创业大赛证书（乡村振兴奖）	10
第七届“互联网+”大学生创新创业大赛证书（校级金奖）	11
省级优秀毕业生证书	12
全国农科研究生乡村振兴志愿者暑期实践活动优秀成果奖	13
《科技小院助推专业硕士研究生培养改革》获优秀管理工作案例	14
全国农科学子联合实践行动“先进工作者”	15
全国农科学子联合实践行动“优秀指导教师”	17
全国农科学子联合实践行动“优秀实践队员”	18
全国农科学子联合实践优秀小队	24
全国农业专业学位研究生实践教学特色基地（多年生稻科技小院）	26
3. 项目课题立项证明及相关材料.....	27
“多年生稻种质资源创新与利用”研究生导师团队.....	27

《现代农业创新与乡村振兴战略》省级研究生优质课程	30
云南大学多年生稻科技小院产教融合研究生联合培养基地	33
4. 学生参与高水平论文.....	35
科技论文 1	35
科技论文 2	48
科技论文 3	59
5. 师生协同产出成果证明.....	68
云南省科学技术奖励（技术发明一等奖）证书	68
云南省科学技术奖励（自然科学二等奖）证书	69
《科技小院—助推边疆地区乡村振兴》封面目录	70
师生发表文章（10 篇）	79
品种审定与专利证书	154
科技小院教师职称晋升及人才称号	159
6. 成果媒体宣传.....	165
7. 其他附件.....	193
多年生稻科技小院培养研究生名单	193
带动建设科技小院清单	194

教学成果评定书

成果名称	基于“多年生稻科技小院”的农学类研究生培养模式改革与实践		
支撑材料	1. 关于组织专家组对云南大学农学院教学成果进行评定的函 2. 云南省教学成果奖（高等教育）申报书 3. 成果相关的获奖证书等附件		
第一完成人	胡凤益	第一完成单位	云南大学
评定时间	2022年8月24日		
<p>专家组评定意见：</p> <p>评定专家组审阅了云南大学农学院提交的“基于‘多年生稻科技小院’的农学类研究生培养模式改革与实践”云南省教学成果奖（高等教育）申报书及相关支撑材料，经过线上质询、讨论和评议，对该成果的理论突破、实践创新和推广应用价值和成果水平评价如下：</p> <p>1. 以服务国家乡村振兴战略需求为导向，以提高学生培养质量促进成长发展为核心，创新了“三农情怀、实践教学、师生协同、创新创业”四轮驱动的农学类研究生人才培养模式：构筑在农村、在田间、在小院的“三在”目标孕育三农情怀，贯彻情怀、事业、实践“三育人”理念实践教学，推进导师成果、学位论文、青年成长“三融合”促进师生协同，实现论文课题、公益研究、创新大赛“三位一体”联动创新创业。构建了基于科技小院模式的应用型人才培养支撑平台，创立了科技小院“一院多点”的轮训培养机制，形成了培养乡村振兴急需的农业人才培养体系，丰富了农业类专业学位研究生培养的有关理论。</p> <p>2. 根据农业专业学位研究生培养的特点，探索了农科研究生培养路径遵循理实并重、第一第二课堂并举、由浅入深和循序渐进的一般规律，强化了多年生稻科技小院为核心支撑的应用型人才培养实践体系，积累了能推广、可复制的农科研究生培养实践经验。</p> <p>3. 实践了基于多年生稻科技小院农学类研究生培养模式，自2015年以来进行深化改革实践，培养了5届42名农科研究生，在云南省带动了花卉、咖啡等</p>			

成果评定书

10个科技小院加快建设，指导学生创新创业作品获得国家级、省部级教育成果7项，师生协同的科研成果获得云南省技术发明一等奖，为云南省农学类研究生培养发挥了积极的引领示范作用，提供了极具推广价值的典型经验和做法。

4. 该成果丰富了科技小院人才培养理论体系，示范应用和实践成效显著，成果丰硕，显著提升了云南省涉农高校农学类研究生的培养效果，具有重要的推广应用价值；该成果处于云南省内领先、国内先进水平。

专家组一致同意通过该成果的评价。

专家组组长签字：

2022年8月24日

教学成果评定专家组组成

专家姓名	工作单位	现从事专业	职称	职务	签字
董维春	南京农业大学	教育经济管理	教授	副校长	
王进军	西南大学	研究生教育	教授	副校长	
王启梁	昆明理工大学	高等教育	教授	副校长	
朱书生	云南农业大学	植物保护	教授	副校长	
江荣风	中国农业大学	资源与环境	教授	院长	



关于组织专家组对云南大学农学院教学成果进行评定的函

各位专家，您好！

云南大学农学院以“多年生稻科技小院”为代表的高原特色农业科技小院人才培养深化综合改革，历经多年实践探索，取得阶段进展；2021年以阶段成果参加第七届中国国际“互联网+”大学生创新创业大赛获得金奖，据此获得直接申报云南省教学成果奖（高等教育）机会。现委托各位专家进行该项教学成果认定（线下会议和通讯评审结合）。特别邀请您担任成果评议专家。

评议的成果材料、评议意见素材稿发送您，附后。

附件 1：拟邀请专家组成员

附件 2：成果评价意见书（讨论稿）



委托联系人：李健强

2022-08-22

附件 1

教育教学成果评价专家组信息

董维春 组长 南京农业大学副校长，教授

王进军 成员 西南大学副校长，教授

王启梁 成员 昆明理工大学副校长，教授

朱书生 成员 云南农业大学副校长，教授

江荣风 成员 中国农业大学 院长，教授

获奖证书

Certificate of Award

李凌宏、李军、唐筱韵、贺汝来、李昆翰、李禹甫、普新援、
黄广一、凌霄

你们的作品《多年生稻——中国粮食安全“新防线”》，在第七届中国国际“互联网+”大学生创新创业大赛中荣获**金奖**

指导老师：胡凤益、黄光福

特发此证，以资鼓励。

主办单位：教育部、中央统战部、中央网络安全和信息化委员会办公室、国家发展和改革委员会、工业和信息化部、人力资源和社会保障部、农业农村部、中国科学院、中国工程院、国家知识产权局、国家乡村振兴局、共青团中央、江西省人民政府

承办单位：南昌大学、南昌市人民政府



中国国际“互联网+”大学生创新创业大赛组织委员会
二〇二一年十月



“健行路”
第七届中国国际“互联网+”
大学生创新创业大赛
2021
The 7th China International College Students "Internet+"
Innovation and Entrepreneurship Competition



编号：2021200051

获奖证书

Certificate of Award

授予：胡凤益、黄光福

第七届中国国际“互联网+”大学生创新创业大赛

优秀创新创业导师

主办单位：教育部、中央统战部、中央网络安全和信息化委员会办公室、国家发展和改革委员会、工业和信息化部、人力资源和社会保障部、农业农村部、中国科学院、中国工程院、国家知识产权局、国家乡村振兴局、共青团中央、江西省人民政府

承办单位：南昌大学、南昌市人民政府



中国国际“互联网+”大学生创新创业大赛组织委员会
二〇二一年十月



编号：2021200051

第十二届 挑战杯
中国大学生
创业计划竞赛



获奖证书

教若寅 王坤 李凌宏 冀高瑞 陈本佳 刘金涛 何速 黄静 胡庆毅 同学

你(们)的项目《 多年生稻科技小院—深入云南边境的乡村振兴稻路 》
在第十二届“挑战杯”中国大学生创业计划竞赛中荣获

铜奖

指导老师：胡凤益 秦世雯 黄光福
特颁此证，以资鼓励。

主办单位：共青团中央 教育部 中国科协 全国学联 黑龙江省人民政府
承办单位：东北林业大学 共青团黑龙江省委



荣誉证书

CERTIFICATE OF HONOR



李凌宏、李军、唐筱韵、贺汝来、李昆翰、李禹甫、普新援、黄广一、凌霄同学：

你们的作品《多年生稻——中国粮食安全“新防线”》，在“俊发杯”第七届云南省“互联网+”大学生创新创业大赛中荣获：

金奖

指导老师：胡凤益、黄光福

特发此证，以兹鼓励！

主办：云南省教育厅

承办：云南大学

协办：俊发集团、云大启迪K栈众创空间、

云南省高等学校创新创业教育指导委员会



二〇二一年十一月



获奖证书

CERTIFICATE OF HONOR

教若寅、王坤、胡庆毅、何迷、黄静、陈本佳、蔡禹瑞、李凌宏、刘金涛 同学：

你们的作品《多年生稻科技小院—深入云南边境的乡村振兴稻路》，在“翰文杯”第六届云南省“互联网+”大学生创新创业大赛中荣获：

银 奖

指导教师：胡凤益、秦世雯、黄光福

特发此证，以兹鼓励。

主办单位：云南省教育厅

承办单位：云南经济管理职业学院

协办单位：云南翰文教育集团、云南省高等学校创新创业教育教育指导委员会、云南省青年红色筑梦之旅联盟、云南九机科技有限公司、杭州沃聚网络科技有限公司

云南省教育厅
二〇二〇年九月



“翰文杯”第六届云南省
“互联网+”大学生创新创业大赛
(青红赛道)

乡村振兴奖

云南省教育厅
二〇二〇年九月



获奖证书



云南大学第七届“互联网+”大学生创新创业大赛

证书编号：106732021005

项目名称：多年生稻——云贵高原梯田“新粮仓”

项目负责人：李凌宏

团队成员：廉美婷、李昆翰、贺汝来、李禹甫、李军、普新援、唐筱韵

赛道：青红赛道

组别：公益组

所在学院：资源植物研究院

指导教师：胡凤益、黄光福

获奖级别：**校级金奖**



云南大学创新创业学院
二〇二一年九月

李凌宏 同学：

你被评为云南省 2022 年

省级优秀毕业生。

特发此证，以资鼓励。

**立志做有理想、
有道德、有文化、有
纪律、有本领、有担
当的社会主义建设者
和接班人，为建设中
国特色社会主义事业
而奋斗！**



中共云南省委教育工委
云南省教育委员会
二〇二二年六月



荣誉证书

CERTIFICATE OF HONOR



为表彰2021年全国农科研究生志愿者暑期
实践活动优秀成果奖获得者，特颁发此证书。

成果名称：走进乡土乡村，致力乡村振兴

获奖者：李凌宏 张树竹 李禹甫 王蕊嘉

指导教师：何飞飞 黄光福 陈蕊

完成单位：云南大学

获奖等级：二等奖

证书编号：NAGVSU-2021025

全国农业专业学位研究生教育
指导委员会秘书处

秘书处

1100000173727

全国农科研究生志愿服务

联盟秘书处

秘书处

3411260131774

二〇二一年十二月五日



昆明学院
KUNMING UNIVERSITY

荣誉证书

证书编号：NLC-MAE2021 YXAL021

吴学尉 胡凤益 刘海英 何飞飞 黄光福 同志：

您撰写的《科技小院助推专业硕士研究生培养改革》，获2021年全国农林院校研究生教育管理研修班暨农林研究生教育助力乡村振兴学术年会优秀管理工作方案例。

特颁此证！

中国学位与研究生教育学会农林学科工作委员会
 全国农业专业学位研究生教育指导委员会秘书处
 农林学科工作部 2021年5月21日 证书处



荣誉证书

胡凤益:

荣获2016年至2020年全国农科学子联合实
践行动

先进工作者

特发此证，以资鼓励。





荣誉证书

陈蕊:

荣获2016年至2020年全国农科学子联合实
践行动

先进工作者

特发此证，以资鼓励。





荣誉证书

秦世雯:

荣获2016年至2020年全国农科学子联合实
践行动

优秀指导教师

特发此证，以资鼓励。

中国作物学会

二〇二一年四月



荣誉证书

何迷:

荣获2016年至2020年全国农科学子联合实
践行动

优秀实践队员

特发此证，以资鼓励。

中国作物学会

二〇二一年四月



荣誉证书

张树竹:

荣获2016年至2020年全国农科学子联合实
践行动

优秀实践队员

特发此证，以资鼓励。





荣誉证书

李凌宏:

荣获2016年至2020年全国农科学子联合实
践行动

优秀实践队员

特发此证，以资鼓励。

中国作物学会

二〇二一年四月



荣誉证书

敖若寅:

荣获2016年至2020年全国农科学子联合实
践行动

优秀实践队员

特发此证，以资鼓励。





荣誉证书

王坤:

荣获2016年至2020年全国农科学子联合实
践行动

优秀实践队员

特发此证，以资鼓励。

中国作物学会

二〇二一年四月



荣誉证书

宁敏:

荣获2016年至2020年全国农科学子联合实
践行动

优秀实践队员

特发此证，以资鼓励。



相关证书

成 果 曾 获 奖 励 情 况	获 奖 时 间	奖 项 名 称	获 奖 等 级	授 奖 部 门
	2017 年	“全国农科学子脱贫攻坚”暑期社会实践活动优秀团队 (指导教师: 胡凤益、陈蕊)	国家级	团中央
	2018 年	2018 年度全国农科学子联合实践优秀小队 (指导教师: 胡凤益、陈蕊)	省部级	中国作物学会 作物学人才培养与教育专业委员会

证明材料:

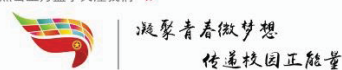
1. 2017 年“全国农科学子脱贫攻坚”暑期社会实践活动优秀团队

× 资讯 | 2017年“全国农科学子脱... ...

资讯 | 2017年“全国农科学子脱贫攻坚”暑期社会实践活动总结通报公示

学校共青团 2017-12-29 11:47 发表于北京

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2017年6月, 团中央学校部组织开展了**2017年“全国农科学子助力脱贫攻坚”暑期实践专项活动**。为汇集、展现和传播“三下乡”社会实践活动成果, 经初审、专家评定等环节, 遴选出144支优秀团队。

坪农场实践团

新疆农业大学农学院赴伊犁实践团

扬州大学农学院阳光协会赴安徽金寨大别山实践团

云南大学农学院会泽实践团

云南大学农学院勐海实践团

云南农业大学农学与生物技术学院赴澜沧县实践团

云南农业大学农学与生物技术学院赴南华、姚安县实践团

云南农业大学农学与生物技术学院赴镇雄县实践团

浙江大学农学院赴五省十一市精准扶贫社会实践团

2. 2018 年度全国农科学子联合实践优秀小队





全国农业专业学位研究生实践教育

培育基地

云南大学多年生稻科技小院实践教育基地

(2021-NYPYJD-07)

有效期至 2024 年 12 月

全国农业专业学位研究生教育指导委员会

二〇二一年十二月



云南省学位委员会 文件 云南省教育厅

云学位〔2021〕17号

云南省学位委员会 云南省教育厅关于公布 2021年度云南省研究生导师团队 建设项目名单的通知

各研究生培养单位：

根据《云南省学位委员会办公室关于开展2021年度研究生导师团队建设项目申报工作的通知》（云学位办〔2021〕11号）要求，经各研究生培养单位推荐、省学位委员会办公室审核和公示等程序，决定立项建设116个省级研究生导师团队（具体名单见附件）。

项目课题立项证明及相关材料

项目建设期限为2年，每个导师团队在建设期限内由申报单位投入经费不少于5万元进行建设。各培养单位要严格按照《云南省研究生导师团队建设管理实施方案》要求，确保建设经费投入，加强经费管理，督促项目负责人切实加强导师团队建设质量，全面提高全省研究生导师队伍整体水平。

附件：2021年度云南省研究生导师团队建设项目名单



(此件公开发布)

附件

2021年度云南省研究生导师团队建设项目名单

序号	团队名称	学校名称	所在学科 (专业学位类别)	团队 带头人
1	人口资源与环境经济学博士生导师团队	云南大学	理论经济学	张国胜
2	中国近现代史与党史基本问题研究博士生导师团队	云南大学	马克思主义理论	张巨成
3	中国现当代文学研究博士生导师团队	云南大学	中国语言文学	张志平
4	运筹学博士生导师团队	云南大学	数学	李建平
5	手性合成化学博士生导师团队	云南大学	化学	邵志会
6	动物学科博士生导师团队	云南大学	生物学	罗静
7	水资源与水灾害博士生导师团队	云南大学	地理学	刘时银
8	机器人与智能系统博士生导师团队	云南大学	通信与信息工程	陶大鹏
9	数据科学与人工智能博士生导师团队	云南大学	计算机科学与技术	岳昆
10	旅游管理博士生导师团队	云南大学	工商管理	田卫民
11	经济民族学硕士生导师团队	云南大学	民族学	郑宇
12	区域水土资源-环境演变与国土空间优化管控硕士生导师团队	云南大学	地理学	赵筱青
13	横断山区灾害性天气气候发生机理及预测硕士生导师团队	云南大学	大气科学	杨若文
14	岩浆岩与内生金属矿床硕士生导师团队	云南大学	地质学	谈树成
15	多年生稻种质资源创制与应用硕士生导师团队	云南大学	作物学	胡凤益
16	视觉媒体与文化计算硕士生导师团队	云南大学	计算机科学与技术	徐丹
17	网络空间安全硕士生导师团队	云南大学	网络空间安全	姚绍文
18	高原遥感博士生导师团队	昆明理工大学	测绘科学与技术	唐伯惠
19	矿山岩土灾害与固废生态资源化博士生导师团队	昆明理工大学	矿业工程	王光进

云南省学位委员会 文件 云南省教育厅

云学位〔2021〕16号

云南省学位委员会 云南省教育厅关于公布 2021年度云南省研究生优质课程 建设项目名单的通知

各研究生培养单位：

为贯彻落实《教育部关于改进和加强研究生课程建设的意见》（教研〔2014〕5号），根据《云南省学位委员会办公室关于做好2021年度云南省研究生优质课程项目申报工作的通知》（云学位〔2020〕8号）要求，经各研究生培养单位评审推荐、省学位委员会办公室审核和公示等程序，决定立项建设云南大学等12

项目课题立项证明及相关材料

个研究生培养单位的 98 门研究生优质课程（以下简称优质课程，名单见附件）。

项目建设期限为 2 年，每门优质课程在建设期限内由申报单位投入经费不少于 5 万元进行建设。各培养单位要严格按照《云南省研究生优质课程建设实施方案》要求，确保建设经费投入，加强经费管理，督促项目负责人切实提高研究生优质课程建设质量，推动全省研究生课程教学内容、教学模式和教学方法创新。

附件：2021 年度云南省研究生优质课程建设项目名单



（此件公开发布）

附件

2021年度云南省研究生优质课程建设项目名单

序号	课程名称	培养单位	负责人姓名	课程类型 (博士/硕士)	课程类别 (公共学位课/专业学位课)	所属学科(专业学位类别)
1	植物分类与系统学	云南大学	周新茂	硕士	专业学位课	生态学
2	旅游产业经济学	云南大学	吕宛青	硕士	专业学位课	工商管理/旅游管理(专硕)
3	市场营销	云南大学	赵书虹	硕士	专业学位课	工商管理(MBA)
4	运营管理	云南大学	吴奇志	硕士	专业学位课	工商管理(MBA)
5	企业战略管理	云南大学	高核	硕士	专业学位课	工商管理(MBA)
6	金融法原理	云南大学	周昌发	硕士	专业学位课	法学
7	国外马克思主义专题研究	云南大学	袁群	博士	专业学位课	马克思主义理论
8	高等岩石学	云南大学	孙涛	硕士	专业学位课	地质学
9	陆气相互作用研究进展	云南大学	杨启东	硕士	专业学位课	大气科学
10	土地覆被与土地评价	云南大学	陈俊旭	硕士	专业学位课	地理学
11	多元统计分析	云南大学	李会琼	硕士	专业学位课	统计学
12	算法图论	云南大学	李建平	硕士	专业学位课	数学
13	现代农业创新与乡村振兴战略	云南大学	胡凤益	硕士	专业学位课	农业(农艺与种业)
14	材料结构与性能	云南大学	郭洪	博士	专业学位课	材料科学与工程
15	中级微观经济学	云南大学	姚书杰	硕士	专业学位课	理论经济学/金融
16	国际贸易政策与实务	云南大学	胡颖	硕士	专业学位课	国际商务

2022 年度云南大学科教融合研究生培养项目和产教融合研究生联合培养基地项目 立项公示

各研究生培养单位、各项目负责人：

根据 2022 年度“研究生创新人才培养”项目工作要求，经申报人申请、各单位推荐，专家组评审，现将 2022 年度云南大学科教融合研究生联合培养项目和产教融合研究生联合培养基地项目立项情况予以公示。

公示期为 4 月 8 日—4 月 12 日，如有异议，请以书面形式向研究生院质量办实名反映；若无异议，公示期满则自动生效。

联系人：翟梦辉 65033585。



项目课题立项证明及相关材料

20	国际河流与生态安全研究院	0857	资源与环境	云南大学-云南褚氏农业产教融合研究生联合培养基地项目	钟荣华	2年	5万
21	建筑与规划学院	0859	土木水利	云南大学-云南省建筑科学研究院产教融合研究生联合培养基地项目	冉志红	2年	5万
22	建筑与规划学院	0859	土木水利	云南大学-北京中外建建筑设计产教融合研究生联合培养基地项目	徐坚	2年	5万
23	建筑与规划学院	0859	土木水利	云南大学边疆民族地区规划与治理产教融合研究生联合培养基地项目	杨庆	2年	5万
24	化学科学与工程学院	0860	生物与医药	云南大学-云南昊邦制药产教融合研究生联合培养基地项目	韦琨	2年	5万
25	生命科学学院	0860	生物与医药	云南大学-北京协和医学院医学生物学研究所产教融合研究生联合培养基地项目	梁斌	2年	8万
26	资源植物研究院	0951	农业	云南大学多年生稻科技小院产教融合研究生联合培养基地项目	胡凤益	2年	8万
27	资源植物研究院	0951	农业	云南大学-保山比顿咖啡产教融合研究生联合培养基地项目	何飞飞	2年	5万
28	资源植物研究院	0951	农业	云南大学-汉晟丰工业大麻种植产教融合研究生联合培养基地项目	杜光辉	2年	5万
29	资源植物研究院	0951	农业	云南大学-云南省农业科学院产教融合研究生联合培养基地项目	胡凤益 吴学尉	2年	10万
30	资源植物研究院	0951	农业	云南大学-云天化产教融合研究生联合培养基地项目	何飞飞	2年	5万
31	工商管理与旅游管理学院	1251	工商管理	云南大学-云南省能投物流产教融合研究生联合培养基地项目	赵德森	2年	5万

ARTICLE

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OPEN

Neo-functionalization of a *Teosinte branched 1* homologue mediates adaptations of upland rice

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The rice orthologue of maize domestication gene *Teosinte branched 1* (*Tb1*) affects tillering. But, unlike maize *Tb1* gene, it was not selected during domestication. Here, we report that an *OsTb1* duplicate gene (*OsTb2*) has been artificially selected during upland rice adaptation and that natural variation in *OsTb2* is associated with tiller number. Interestingly, transgenic rice overexpressing this gene shows increased rather than decreased tillering, suggesting that *OsTb2* gains a regulatory effect opposite to that of *OsTb1* following duplication. Functional analyses suggest that the *OsTb2* protein positively regulates tillering by interacting with the homologous *OsTb1* protein and counteracts the inhibitory effect of *OsTb1* on tillering. We further characterize two functional variations within *OsTb2* that regulate protein function and gene expression, respectively. These results not only present an example of neo-functionalization that generates an opposite function following duplication but also suggest that the *Tb1* homologue has been selected in upland rice.

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Modern civilization is built on a foundation of domesticated crops and animals that have been the main source of calories for humans for more than 10,000 years. Multiple domesticated crops often share similar domestication traits compared to their wild relatives, such as loss of seed shattering and dormancy, increased fruit size, or alterations of plant architecture; this phenomenon is referred to as domestication syndrome. An increase in apical dominance is an important example of domestication syndrome that occurs in many gramineous crops. Domesticated maize, sorghum, rice, wheat, and foxtail millet all show an increase in apical dominance and a corresponding reduction in shoot branching compared to their wild counterparts¹. The well-established domestication gene *Teosinte branched 1* (*Tb1*) was originally found to result in increased apical dominance in maize². QTLs containing *Tb1* orthologous loci in sorghum, foxtail millet, wheat and pearl millet were later discovered to account for tiller variation under domestication^{3–5}. However, these studies based on QTL analysis do not unequivocally demonstrate whether the underlying causal gene is a *Tb1* orthologue or not. In rice, the *Tb1* orthologous gene *OsTb1*, located on chromosome 3, was shown by mutant analysis to impact tiller branching but was suggested to not be related to rice domestication^{6,7} because this locus was not selected during domestication. A previous whole-genome scan for domestication genes in rice conducted by large-scale genome resequencing also detected no signals for artificial selection around this region^{8,9}. Although it has been realized that the increase in apical dominance constitutes parallel morphological evolution in cereal crops, it remains elusive whether this parallel domestication has a similar genetic basis.

There are two rice subspecies *Oryza sativa japonica* and *indica* that exhibit different tillering abilities, with the *japonica* subspecies tending to have fewer tillers than *indica*. Rice also has two ecotypes, upland and irrigated ecotypes, which are adapted to rainfed upland conditions and well-watered conditions, respectively. Our previous analysis of upland rice genomes and irrigated rice genomes revealed that another gene, which is a paralogue of *OsTb1* located on rice chromosome 9 (hereafter referred to as *OsTb2*), is highly differentiated between the two ecotypes¹⁰. Upland rice varieties are generally *japonica* and tend to exhibit taller plant architecture, better-developed roots and fewer tillers compared to their irrigated counterpart (Supplementary Fig. 1). It has been known that in upland rice fewer tillers is an adaptive architecture because upland varieties with a small number of tillers tend to have longer deep roots and larger panicles than those with profuse tillers^{11,12}. Given that the two ecotypes have apparently different tillering abilities¹⁰, it is tempting to speculate that *OsTb2* might regulate rice tillering.

Gene duplication is a major way whereby new genes originate. *OsTb2* and *OsTb1* are highly homologous and appear to be the two most closely related gene copies in the rice genome that likely diverged from a gene duplication event. After duplication, the new gene copy will be functionally redundant with the old copy in the short term, while in the long term, it can become a pseudogene or may be lost¹³. Alternatively, in some scenarios, the new copy obtains a new function during evolution, a process referred to as neo-functionalization^{14,15}. It is important to test whether *OsTb2* has retained the same function as *OsTb1* in repressing tillering. *DWARF14* (*D14*) is a gene involved in strigolactone signalling and negatively regulates rice tillering¹⁶. Previous studies showed that *OsTb1* represses tillering by interacting with *OsMADS57* to promote *D14* expression¹⁷. Whether *OsTb2* plays a similar role in regulating rice tillering remains to be elucidated.

In this study, we present evidence that *OsTb2* has evolved a function opposite to that of its paralogue *OsTb1*. Unlike *OsTb1*, which is a tillering inhibitor, *OsTb2* is a positive regulator of

tillering. We show that *OsTb2* likely functions by interfering with the inhibitory effect of *OsTb1* on tillering. Moreover, we find that a 3 base pair (bp) indel in the coding region of *OsTb2* is divergent between the *japonica* and *indica* subspecies and that in *japonica*, the 3 bp insertion enhances the function of *OsTb2* in promoting tillering. More interestingly, another functional variation is a T to C mutation that has been selected and fixed in upland rice. By reducing the expression of *OsTb2*, this derived C allele has likely contributed to the dryland adaptation of upland rice by reducing tillers and increasing grain yield per panicle, generating an upland-adaptive plant architecture that was favoured and selected by humans. Our findings not only provide another vivid example of gene neo-functionalization but also demonstrate that paralogous genes with opposite functions might be selected during domestication and breeding.

Results

OsTb2 is differentiated between upland and irrigated rice.

Upland and irrigated rice ecotypes display significant differentiation in tillering ability. In our previous comparative genomic study¹⁰, we found that *Os09g0410500* on chromosome 9, a homologue of the maize *Tb1* gene, was highly differentiated between the two ecotypes. The rice orthologue of the maize *Tb1* gene, *OsTb1*, is located on chromosome 3, showing the highest homology to maize *Tb1* among the rice genes (See Methods). We therefore referred to the *Tb1* homologue on chromosome 9 as *OsTb2*. F_{ST} and XP-CLR were used to assess the artificial selection signature around *OsTb2* (40 kb upstream to 40 kb downstream) (see Methods). Both F_{ST} and XP-CLR displayed a peak signal around *OsTb2*, and the empirical P -values of both tests are below 5% (Fig. 1), indicating *OsTb2* was probably selected during the differentiation of upland *japonica* and irrigated *japonica* rice.

Since high population differentiation of a gene region can be caused by multiple other factors such as allele surfing, hierarchical population structure etc.¹⁸, we further checked the allele frequency spectra of SNPs from the vicinity of the putative causal mutations (see the next section for details about the putative causal mutations). We observed a U-shape pattern of the derived allele frequency spectra (AFS) in upland *japonica*, and the pattern decayed with the increasing distance from the causal mutations (Supplementary Fig. 2), which is a signal of the hitch-hiking effect^{19,20}. We further performed a nonparametric Kolmogorov-Smirnov test to show that with the increasing distance from the focal mutation, the U-shape AFS pattern of SNPs in the sliding windows also decays and become similar to the background AFS pattern (Supplementary Fig. 3), supporting the hitch-hiking event. Moreover, we used the Hudson-Kreitman-Aguadé (HKA) test to screen for genome-wide recently selected genes (see Methods), and *OsTb2* was found to be among the 301 selected genes (HKA test P -value = 0.019). Performing genome scan using the SweeD program also uncovered a significant likelihood value (ranking top 1.6%) in upland *japonica*, but an insignificant likelihood value (ranking top 17.3%) in irrigated *japonica* (Supplementary Fig. 4). These multiple lines of evidences strongly support that *OsTb2* was under selection during the cultivation of upland *japonica* rice. As shown by our previous phylogenetic analysis¹⁰, upland *japonica* evolved from irrigated *japonica*. The artificial selection signature therefore suggested that *OsTb2* might have been selected during evolution from irrigated rice to upland rice. Considering that the *OsTb1* homologues, found in maize and other crops, have been reported to account for the change in apical dominance and that upland rice accessions actually have a significantly lower tillering ability than irrigated accessions¹⁰, we were interested in determining whether *OsTb2* also impacts

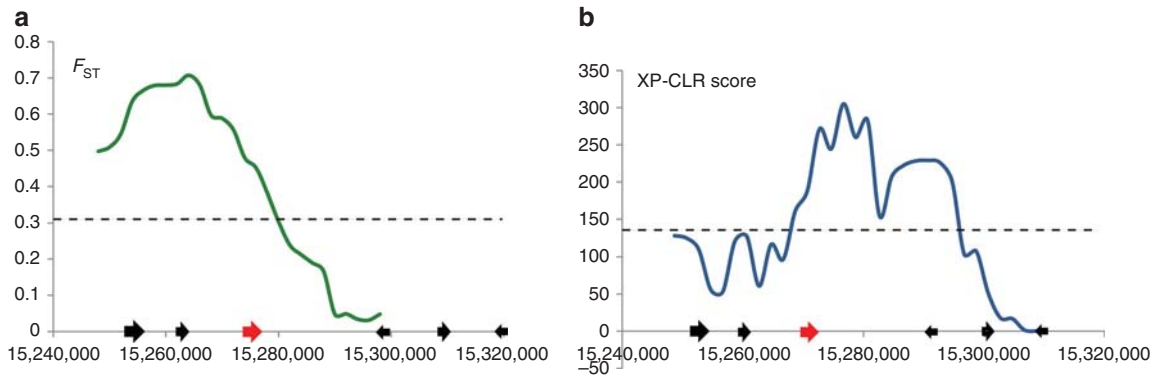


Fig. 1 Artificial selection signal around the *OsTb2* region. Peak signals (red arrows) were found by F_{ST} (a) and XP-CLR (b) assessment, respectively. The artificial selection signals were detected based on the F_{ST} value (a) and the cross-population composite likelihood ratio test (XP-CLR, b). The F_{ST} value and XP-CLR score were calculated window by window (see Methods), and we then choose the windows with genome-wide top 5% values as candidate regions with selection signals. The dotted horizontal lines indicate the threshold of genome-wide top 5% value.

tiller number in rice and whether it was selected during the improvement of upland rice.

***OsTb2* is associated with rice tillering ability.** To identify the polymorphic sites of *OsTb2*, we sequenced this gene in 84 upland and 82 irrigated accessions (Supplementary Data 1) using Sanger sequencing. In total, seven SNPs and two indels were identified (Fig. 2a). To investigate the association between *OsTb2* and tillering ability, we grew 132 of the above sequenced accessions and collected phenotypic data on their tiller numbers at 40 and 50 days after germination (DAG). We then tested the association between the SNPs/indels and tiller number phenotypes. As shown in Table 1, among the nine polymorphic sites, only Indel I and SNP3 were significantly associated with tiller number at both 40 DAG and 50 DAG. Moreover, these associations presented the smallest *P*-values among all the variants, indicating that Indel I and/or SNP3 is likely to be the functional variant(s) (Table 1). The two variants produce three haplotypes (Fig. 2b). Considering that hitch-hiking variants tightly linked with causal variants also have the potential to be associated with phenotypes, it remains to be determined whether only one or both variants are functional.

Association analysis can sometimes yield a false-positive result due to population structure²¹. Thus, we further tested the association between *OsTb2* alleles and tiller number in segregating populations. We used an F_8 recombinant inbred line (RIL) population obtained by crossing the upland variety IRAT104 and the irrigated variety IR64, which segregate for both the Indel I and SNP3 markers. We genotyped the 134 lines in the F_8 RIL populations using derived cleaved amplified polymorphic sequence (dCAPS) markers²² (see Methods) and grew those lines in irrigated and upland conditions to observe their phenotypes. Severely distorted segregation phenomena were observed for both Indel I and SNP3 loci. For the Indel I locus, 32 lines had a 3bp+ (3 bp insertion) genotype, while 96 lines had a 3bp- (3 bp deletion) genotype (the other six lines were heterozygous). When tiller numbers were compared between the Indel I-3bp+ lines and Indel I-3bp- lines, we observed a significant increase in tillers for the Indel I-3bp+ lines compared to lines with the Indel I-3bp- genotype (Student's *t*-test, $P = 0.039$; Table 2). For the SNP3 site, the RIL- F_8 population was so skewed towards SNP3-T that we found only four lines with SNP3-C, making it difficult to statistically test its association with tiller number. However, we found one individual, RIL116, that was heterozygous for both Indel I and SNP3. Therefore, we selfed this individual to produce a near-isogenic F_2 population segregating for both Indel I and SNP3.

The derived near-isogenic F_2 population included 451 individuals, all of which were grown to be phenotyped and genotyped. In this near-isogenic F_2 population, distorted segregation was also observed for SNP3. Among the 451 individuals, we identified 135 individuals with the SNP3-T genotype, but only 60 individuals with the SNP3-C genotype, and the rest were heterozygous. For Indel I, 60 homologous 3bp- individuals and 75 homologous 3bp+ individuals were genotyped. All of these individuals were phenotyped twice (40 and 50 DAG). A conditional association study was then conducted to examine the association between SNP3/Indel I and tiller number. The results showed that the SNP3-C genotype had significantly fewer tillers than did the SNP3-T genotype under the Indel I-3bp+ condition (Student's *t*-test, $P = 6.15E-05$ at 50 DAG; Table 3), while Indel I-3bp+ plants had significantly more tillers than Indel I-3bp- plants (Student's *t*-test, $P = 0.0193$ at 50 DAG; Table 3). This result further confirmed that the derived Indel I-3bp+ allele in *japonica* corresponded to an increase in tiller number, while the derived SNP3-C allele in upland *japonica* was associated with a reduced number of tillers. The findings that at 40 DAG, the SNP3 locus, but not the Indel I locus, was marginally significantly associated with tiller number (Student's *t*-test, $P = 0.1191$; Table 3) and that the Indel I locus became significant only at 50 DAG suggested that, consistent with what we observed in the natural population association study, SNP3 might exhibit a function around the early tillering stage (40 DAG) and that Indel I probably affects tillering around the late tillering stage (50 DAG).

***OsTb2*^{3bp+} can increase rice tiller number.** We examined *OsTb2* expression patterns in different tissues at 40 DAG and 50 DAG stages using qRT-PCR. The results showed that *OsTb2* was predominantly expressed in the basal tiller node with a relatively lower expression in leaf blade and sheath. Higher expression of *OsTb2* in the basal tiller node at 40 DAG than 50 DAG indicated that *OsTb2* starts to function from the early stage of tillering (Supplementary Fig. 5). To validate the function of *OsTb2*, we cloned the gene sequences of IRAT104 (*OsTb2*^{3bp+}) and IR64 (*OsTb2*^{3bp-}) into the overexpression vector pCUBI-1390, driven by the *Ubiquitin* promoter, which was then transformed into *Nipponbare*. Multiple positive transgenic lines were obtained by hygromycin B screening. Gene expression was greatly increased in the *OsTb2*^{3bp+}-OE1~6 and *OsTb2*^{3bp-}-OE1~6 lines compared to the control lines, as shown in Supplementary Fig. 6a. Two transgenic lines for each genotype as well as control lines (both negative lines and WT) were then planted in dryland and irrigated environments in two growth seasons for phenotypic

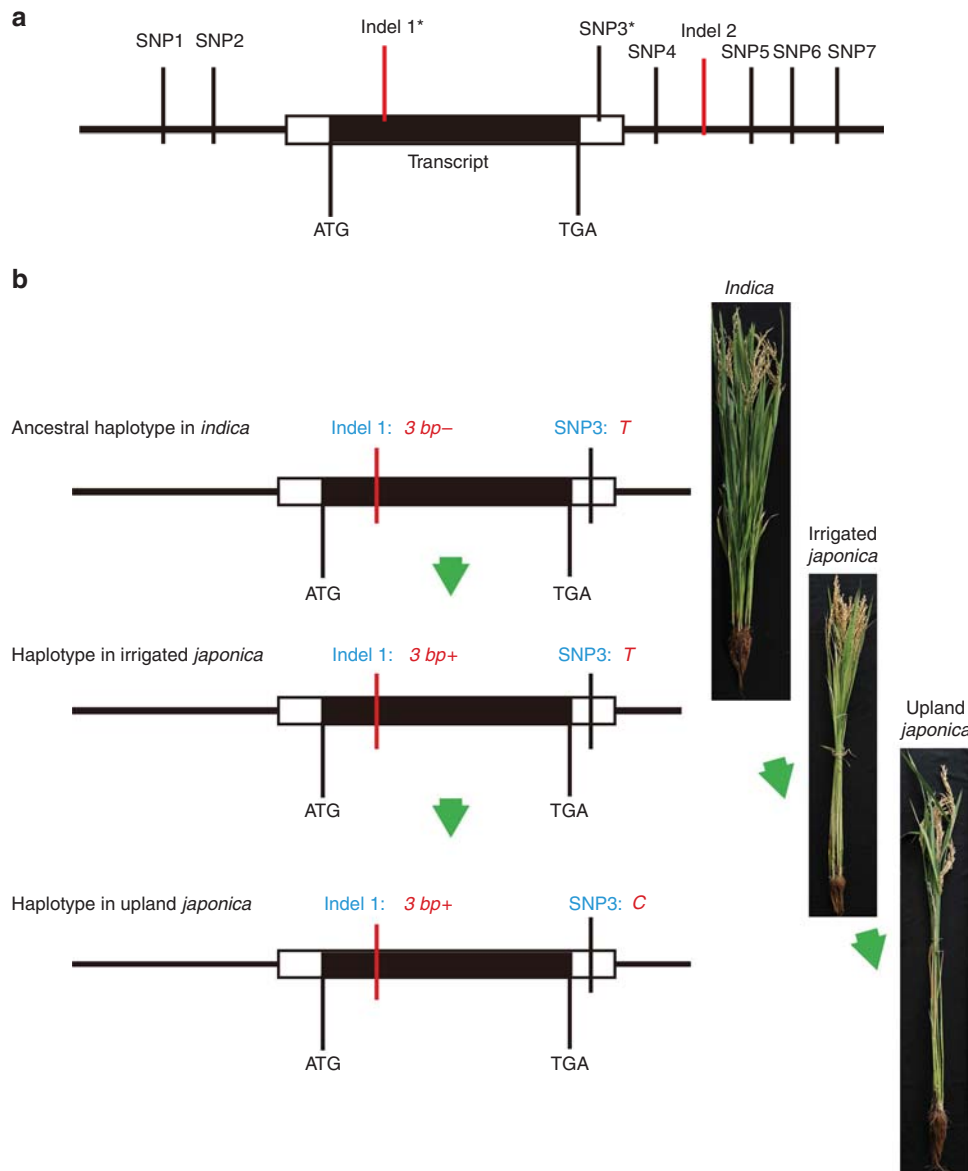


Fig. 2 Variants and haplotypes of *OsTb2*. **a** Structure and polymorphic sites of *OsTb2*. Two indels and seven SNPs were found in the *OsTb2* gene. Indel 1 and SNP3 (bold with asterisk) are both significantly associated with tiller numbers. **b** Indel 1 and/or SNP3 in the *OsTb2* gene may be functional variants for which three haplotypes were observed in the germplasm. The 3bp-/T haplotype is present in *indica* and wild rice, and thus likely to be the ancestral haplotype. The 3bp+/T haplotype is mainly found in irrigated *japonica*, and the 3bp+/C haplotype is specific to upland *japonica*, consistent with the evolutionary viewpoint that upland *japonica* evolved from irrigated *japonica*.

Table 1 Association between *OsTb2* polymorphic sites and tiller numbers.

Polymorphic sites	Position on chr09	Segregating genotypes	P-value ^a (40 DAG)	P-value (50 DAG)
SNP1	15272303	C/T	0.08713	0.5717
SNP2	15272752	G/A	0.07238	0.8106
indel1	15273436-15273438	3bp+/3bp- ^b	0.01099	1.30E-11
SNP3	15274099	T/C	3.80E-05	2.55E-12
SNP4	15274295	T/C	0.4748	0.0003731
indel2	15274601-15274603	3bp+/3bp-	0.3998	5.88E-08
SNP5	15274707	G/A	0.2722	1.38E-08
SNP6	15274798	C/T	rare SNPs	rare SNPs
SNP7	15274921	G/A	0.2306	9.45E-07

Source data are provided as a Source Data file.

^aFor each polymorphic site, we divided the accessions into two homozygous groups. Students' t-test was then used to assess the differences in tiller numbers and determine significant P values between two groups. Indel 1 and SNP3 are significantly associated with tiller numbers at both 40 DAG and 50 DAG. The effect sizes are shown in Supplementary Table 1.

^b3bp+ refers to the three base pair insertion; 3bp- refers to the three base pair deletion. The positions on Chr09 are in reference to genome version IRGSP 5.0.

Table 2 Conditional analysis for Indel I and SNP3 in natural and F₈-RIL populations.

Analysis	Natural population		F ₈ -RIL population	
	Comparison of Indel I-3bp+ with Indel I-3bp- conditioning on SNP3-T	Comparison of SNP3-T with SNP3-C conditioning on Indel I-3bp+	Comparison of Indel I-3bp+ with Indel I-3bp-	Comparison of Indel I-3bp+ with Indel I-3bp- conditioning on SNP3-T
P-value (40 DAG)	0.6954	0.0069	0.1343	0.1509
Mean value difference	4.17%	29.50%	12.70%	14.50%
Variance	9.1	8.4	9.4	9.9
Effect size	0.17	3.22	0.62	0.72
P-value (50 DAG)	1.60E-05	0.0003	3.90E-02	0.2032
Mean value difference	30.70%	32.10%	11.20%	6.50%
Variance	81.3	44.9	43.9	40.2
Effect size	5.02	3.47	1.41	0.78
Tiller number comparison	Indel I-3bp+ < ^a Indel I-3bp-	SNP3-C < SNP3-T	Indel I-3bp+ > ^b Indel I-3bp-	Indel I-3bp+ > Indel I-3bp-

Source data are provided as a Source Data file.
^aLess than.
^bMore than.

Table 3 Conditional analysis for Indel I and SNP3 in a near-isogenic F₂ population.

Analysis	Comparison of Indel I-3bp+ with Indel I-3bp- conditioning on SNP3-T	Comparison of SNP3-T with SNP3-C conditioning on Indel I-3bp+
P-value (40 DAG)	0.3724	1.19E-01
Mean value difference	7.59%	12.90%
Variance	19.5	13.1
Effect size	0.47	0.82
P-value (50 DAG)	0.02	6.15E-05
Mean value difference	15.40%	22.80%
Variance	70.9	45.1
Effect size	1.64	2.77
Tiller number comparison	Indel I-3bp+ > ^a Indel I-3bp-	SNP3-C < ^b SNP3-T

Source data are provided as a Source Data file.
^aMore than.
^bLess than.

examination. Accordingly, it was found that the transgenic lines overexpressing *OsTb2^{3bp+}* had significantly more tillers than the control lines (Fig. 3 and Supplementary Fig. 6b, c), supporting the hypothesis that unlike its homologue *Tb1*, which is a tiller suppressor, *OsTb2* is a tiller enhancer. The transgenic lines overexpressing *OsTb2^{3bp-}* had slightly fewer (but not significantly) tillers, implying that the *OsTb2^{3bp-}* genotype had a limited effect on tiller number.

Irrigated *japonica* often has fewer tillers than irrigated *indica* rice likely due to their different genetic composition. Our transgenic experiments showed that the *japonica*-specific *OsTb2^{3bp+}* could partially increase tiller number (Fig. 3b, d) and thus could alleviate tiller suppression by other genes in the *japonica* background. This allele might have been fixed in *japonica* because it could alleviate tiller suppression or due to random genetic drift.

Indel I alters *OsTb2*'s regulatory effects on *D14* expression. We then wondered how the Indel I mutation might alter the function of *OsTb2* in affecting tiller number. Considering that Indel I-3bp+ causes a single amino acid insertion in the TCP binding domain of this *OsTb2* transcription factor and that in silico prediction

hinted that this insertion might have changed the peptide secondary structure (Supplementary Fig. 7), we hypothesized that I-3bp+ may have altered the function of *OsTb2* by altering its structure.

As our data showed that *OsTb2^{3bp+}* had a function (i.e., promoting tillering) antagonistic to the *Tb1* orthologue *OsTb1*, we next asked whether *OsTb2* influenced gene expression in an opposite manner. To determine whether the 3 bp insertion affected the function of the *OsTb2* transcription factor, we carried out a transient expression assay using a luciferase reporter system. *D14* expression could promote apical dominance and reduce tillers. We found that the extent of *D14::LUC* expression was reduced by cotransformation with *OsTb2* (Fig. 4a). The transient expression assays showed that both *OsTb2^{3bp+}* and *OsTb2^{3bp-}* indeed impacted the expression of *D14*, and *OsTb2^{3bp+}* exerted a significantly greater inhibitory effect than *OsTb2^{3bp-}* (Fig. 4a). It was previously shown that *OsTb1* represses tillering by increasing the expression of *D14*. Therefore, it is likely that *OsTb2* represses *D14* by counteracting the positive regulation of *D14* transcription by *OsTb1*. The yeast one-hybrid (Y1H) assay verified that *OsTb2* could not bind to *D14* promoter directly (Fig. 4c), which implied that *OsTb2* reduced expression in other ways. To determine how

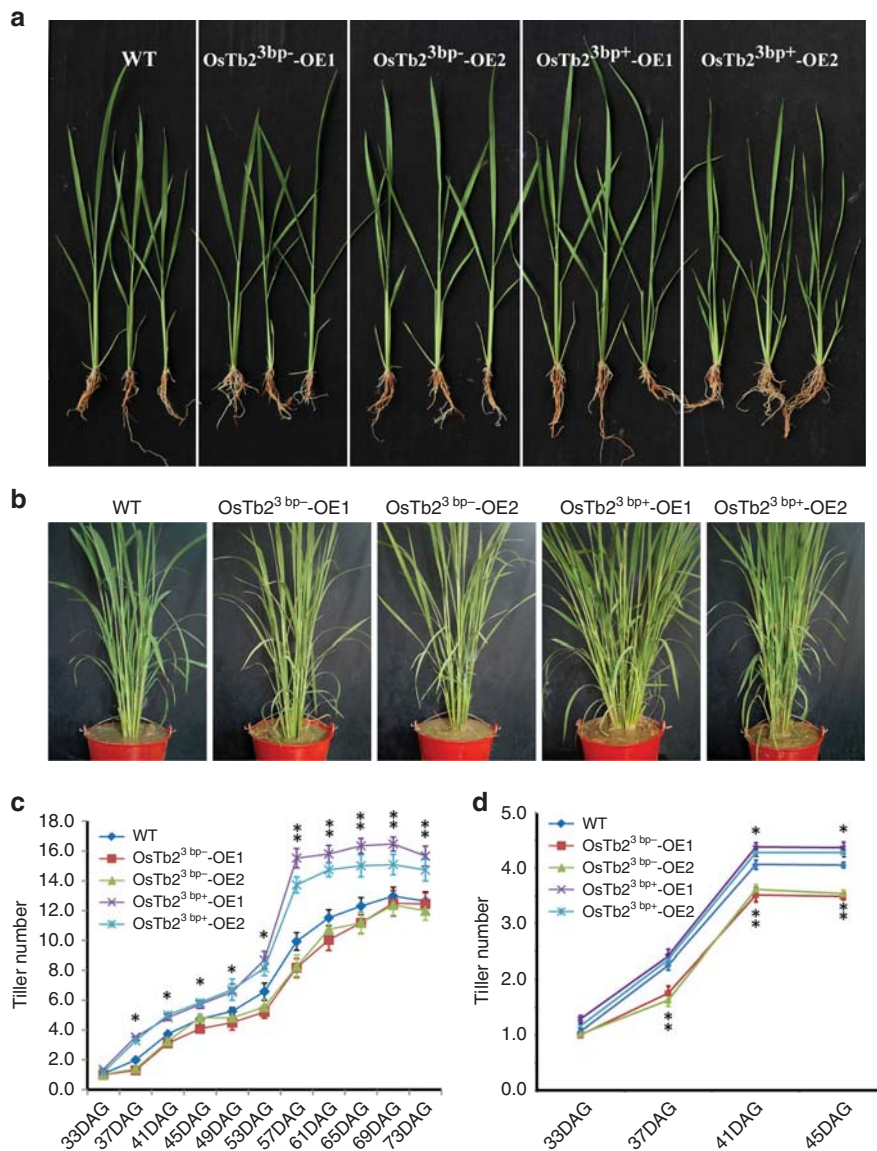


Fig. 3 *OsTb2*^{3bp+} can positively regulate rice tillering. **a** Phenotypes of transgenic plants overexpressing two genotypes (3 bp+ and 3bp-) of *OsTb2* at 30 DAG under irrigated conditions. WT, wild type. **b** Phenotypes of transgenic plants overexpressing two genotypes of *OsTb2* at 65 DAG under irrigated conditions. WT, wild type. **c** Tiller number of transgenic plants overexpressing both *OsTb2*^{3bp+} and *OsTb2*^{3bp-} at different DAG under irrigated conditions. **d** Tiller numbers of transgenic plants overexpressing both *OsTb2*^{3bp+} and *OsTb2*^{3bp-} at different DAT under dryland conditions. Each value in c, d represents the mean ± s.d. (n = 50 plants). Student's *t*-test analysis indicated a significant difference (compared with the WT control, **P* < 0.05, ***P* < 0.01).

OsTb2 repressed *D14* expression, transient expression assays were further used to test whether *OsTb2* plays a role in repressing *D14* via the *OsTb1*-*OsMADS57* pathway. When *OsTb2* was coexpressed with *OsTb1* and *OsMADS57*, the expression of the cotransformed reporter gene *D14pro::LUC* indicated that *OsTb2* may neutralize the inhibition of *OsTb1* on *OsMADS57*, which directly binds the *D14* promoter to inhibit its transcription (Fig. 4b, d). The results also showed that the two Indel I genotypes resulted in significant differences in *D14* expression (Student's *t*-test, $P_{OsTb2} = 0.0218$, Fig. 4a): the 3bp+ genotype corresponded to a lower level of *D14*, which was consistent with the 3bp+ genotype yielding more tillers. Therefore, we concluded that *OsTb2* reduces the expression of *D14*, which then consequently increase tiller number. The 3 bp insertion that occurred in *japonica* promoted the repression of *D14* by *OsTb2*, thus representing a genotype yielding an increased tiller number.

***OsTb2* binds to *OsTb1* and offset *OsTb1*'s tiller suppression.** TCP genes encode plant-specific transcription factors with a bHLH motif that allows DNA binding and protein-protein interactions, forming homodimers or heterodimers^{23,24}. Therefore, we asked whether *OsTb1* interacts with *OsTb2* in planta. BiFC assays indicated that the interaction between *OsTb2* and *OsTb1* occurred in the *Nicotiana benthamiana* nucleus (Fig. 5), which was consistent with the nuclear subcellular localization of *OsTb2* (Supplementary Fig. 8). Therefore, *OsTb2* was able to form a heterodimer with *OsTb1*. CoIP tests revealed that the protein complexes pulled down using anti- α -GFP agarose were recognized by an anti- α -MYC antibody in lines cotransformed with GFP-*OsTb2* and MYC-*OsTb1* (Fig. 5); i.e., *OsTb2* could bind to *OsTb1* in planta. It was previously found that *OsTb1* represses tillering by increasing the expression of *D14*¹⁷. Therefore, *OsTb2* probably represses *D14* expression by counteracting

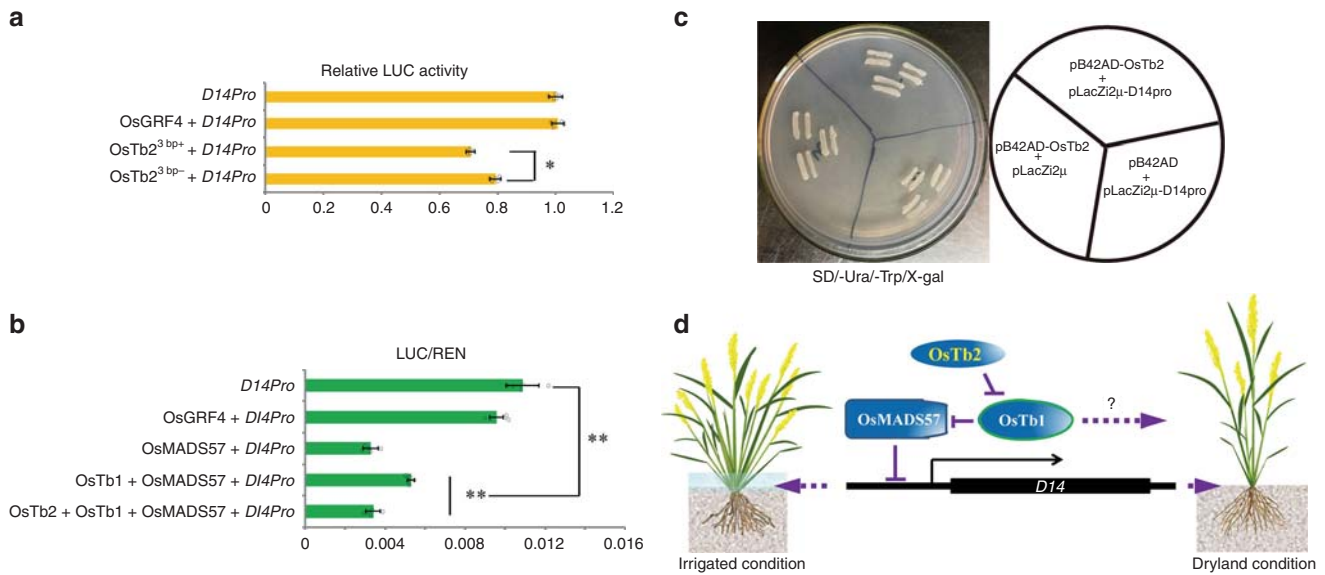


Fig. 4 *OsTb2*^{3bp+} negatively regulates *D14* via the *OsTb1-OsMADS57-D14* pathway. **a** Effects of *OsTb2*^{3bp+} and *OsTb2*^{3bp-} on the transcriptional regulation of *D14* in rice protoplasts. **b** Effects of *OsTb2*^{3bp+} on the transcriptional regulation of *D14* via the *OsTb1-OsMADS57-D14* pathway in *Nicotiana benthamiana*. *OsGRF4* is used as a negative control for detecting the effects of *OsTb2* on *D14pro::LUC* activity. Each relative luciferase activity of *D14pro::LUC* value in a and b represents the mean \pm s.d. ($n = 10$ biologically independent samples). Student's *t*-test analysis indicated a significant difference ($*P < 0.05$, $**P < 0.01$). **c** In the yeast one-hybrid assay, *OsTb2* fusion proteins fail to activate *D14pro::LacZ* reporter gene expression in yeast. The right diagrammatic drawing indicates the yeast strains transformed with related plasmids. **d** A schematic model depicts that *OsTb2* interacts with *OsTb1* to regulate the expression of *D14*. *OsMADS57* directly represses the expression of *D14*; *OsTb2* interacts with *OsTb1* to alleviate *OsTb1*'s inhibition on *OsMADS57*, which consequently reduces the expression of *D14* and increases tillers.

the positive regulatory effect of *OsTb1* on *D14*, ultimately increasing tiller number.

SNP3 C-allele confers reduced *OsTb2* expression and tillers. Since SNP3 causes a mutation in the 3'UTR of the *OsTb2* transcript, it is likely that this SNP might alter the expression level of this gene. To determine whether the SNP3 in 3'UTR contribute transcription regulation of *OsTb2*, we grew 39 rice lines with different SNP3 genotypes and checked the expression of *OsTb2* in the tillering node at 40 DAG and 50 DAG (Supplementary Data 2). C-type cultivars consistently showed significantly lower *OsTb2* expression at 50 DAG under both dryland (soil water content, 16.8%) and irrigated conditions (Fig. 6a), suggesting that C-allele of SNP3 reduce the expression of *OsTb2* (Fig. 6a). Consistently, C-type lines produce significantly fewer tillers at both 40 DAG and 50 DAG than T-type lines under both irrigated and dryland conditions (Fig. 6b). Pearson correlation analysis showed that the expression level of *OsTb2* is significantly positively correlated with tiller number at 50 DAG under dryland (Fig. 6c, Student's *t*-test, $P = 0.003$; $R = 0.48$) and irrigated (Fig. 6d, Student's *t*-test, $P = 0.044$; $R = 0.35$) conditions. Fewer tillers in upland rice represent an adaptive trait because it increases the root/shoot ratio^{25,26} and results in longer deep roots as well as larger panicles^{11,12}. To examine whether the C-allele of *OsTb2* selected in upland rice brings about higher grain yield per panicle. We compare the grain yield per panicle data collected in the past three growth seasons between C-type and T-type lines. The results consistently showed that C-type allele is significantly associated with larger yield per panicle in all three growth season under dryland condition (Fig. 6e). We also conducted Pearson Correlation Analysis for the expression of *OsTb2* and yield data (see Methods). We found that *OsTb2* expression is negatively correlated with yield per panicle (Fig. 6f; Student's *t*-test, $P = 0.08$, $R = 0.29$), consistent with our findings that the lower *OsTb2* expression confers by the C-allele results in higher yield per

panicle under dryland condition. We also tried to examine the correlation between SNP3 and gene expression using our RILs by growing 12 lines in irrigated and dryland conditions in the 2nd season of 2017. However, unfortunately, the dryland came across an extreme drought (soil water content 8.1% at 50 DAG) in that season. As shown in Supplementary Figure 9, we observed the C-allele corresponds to lower gene expression in irrigated conditions, consistent with what we observe in Fig. 6. But unexpectedly, we saw a rapid induction of the C-allele in the extreme drought (Supplementary Fig. 9). We speculated that the extreme drought might have triggered another feedback pathway to compensate the over-suppression of tillering (Supplementary Fig. 9b). The detailed mechanism for this *OsTb2* induction under extreme drought remains to be elucidated by future studies.

Discussion

Plants modify their development to adapt to the environment, protecting themselves from detrimental conditions by triggering a variety of signalling pathways²⁷. Axillary buds are indeterminate structures that can be developmentally controlled in response to endogenous or environmental cues²⁸. *OsTb2* from our study is identical to the *RETARDED PALEA1* gene reported in a previous study, which showed that this gene plays a role in palea development and floral zygomorphy in rice²⁹. In the present study, we comprehensively analysed the function of *OsTb2* and showed that *OsTb2* modulates the development of axillary buds and was artificially selected during the adaptation of upland rice. Our transgenic experiments and association analysis supported the hypothesis that contrary to *OsTb1*, *OsTb2* suppresses apical dominance and counteracts tillering inhibition by *OsTb1*, leading to an increased tiller number. We found two functional mutations in *OsTb2*, i.e. the 3bp indel-I that distinguishes *japonica* and *indica* subspecies and the SNP3 that differentiates upland *japonica* and irrigated rice (including irrigated *japonica* and *indica*).

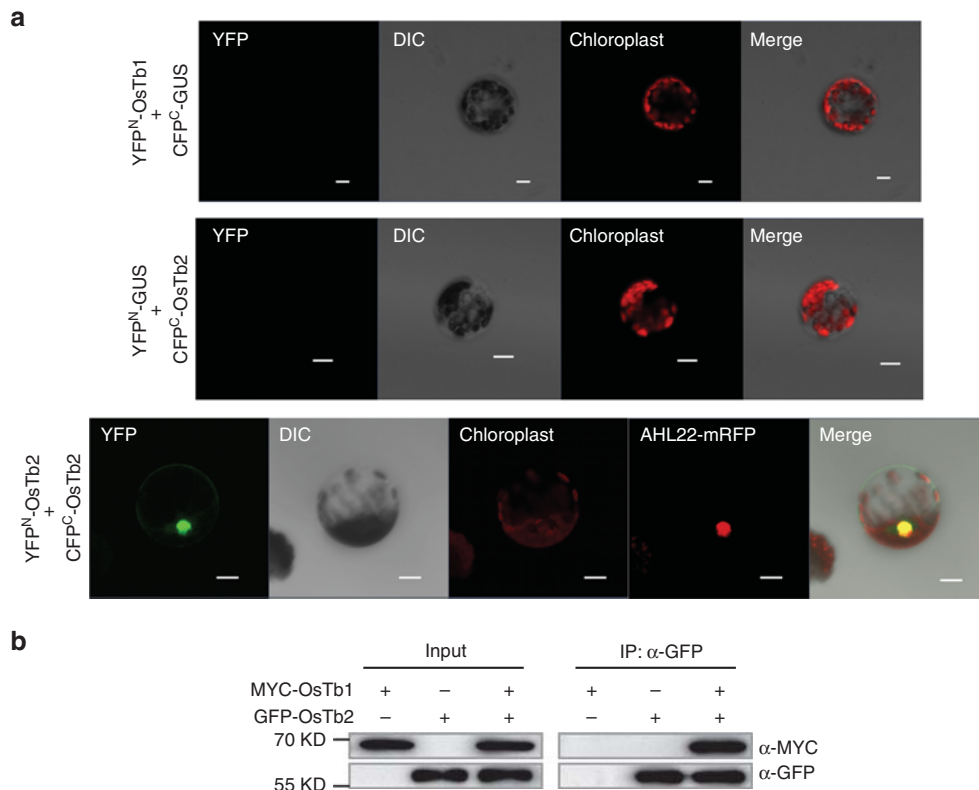


Fig. 5 OsTb2 interacts with OsTb1 in the nucleus. **a** YFP^N-OsTb1 and CFP^C-OsTb2 were expressed in a pairwise manner in rice protoplasts and exhibited a direct interaction in the nucleus, in which AHL22-mRFP was used as the nuclear marker protein; CFP^C-GUS and YFP^N-GUS fusion proteins were used as negative controls and were coexpressed with YFP^N-OsTb1 and CFP^C-OsTb2, respectively, in rice protoplasts. DIC indicates differential interference contrast transmission; the merged image is also shown; scale bar, 20 μm. **b** Coimmunoprecipitation assays of OsTb1 and OsTb2. Protein extracts from rice protoplasts harbouring MYC-OsTb1 and GFP-OsTb2 were coimmunoprecipitated by anti-GFP beads and detected by anti-GFP and anti-MYC antibodies. Protoplasts transformed with single MYC-OsTb1 or GFP-OsTb2 were used as a negative control. The source data underlying Fig. 5b are provided as a Source Data file.

In general, *japonica* rice exhibits fewer tillers than *indica* rice, and our data showed that the *japonica*-specific *OsTb2*^{3bp+} genotype could increase the number of tillers, while the *indica*-species *OsTb2*^{3bp-} genotype could not. This mutation was probably fixed in *japonica* rice because it could alleviate tiller suppression by other genes in the *japonica* background or due to random genetic drift. We've shown using transient expression assays that *OsTb2*^{3bp+} and *OsTb2*^{3bp-} alleles encode proteins with different activities on *D14* expression likely by affecting OsTb2 protein activity (Fig. 4a). Also, using in silico prediction, we showed that this *indel* variant would alter the protein secondary structures of OsTb2, which likely affects its function (Supplementary Fig. 7).

The upland rice ecotype evolved from irrigated *japonica* rice¹⁰ and adapted to rainfed upland conditions. It has long been well established that in upland rice fewer tillers is an adaptive trait. For example, Fukai et al. screened 1081 rice lines and found that well-adapted upland rice tends to have a small number of well-developed tillers. These lines developed a few large tillers with longer roots¹¹, while the lines with profuse tillers tend to have shorter roots and their tillers were not well developed under upland conditions. Also, Kato et al. examined the rice lines adapted to aerobic dryland soils and found that plant architecture with a few large tillers is a more suitable architecture than that with profuse tillers¹². Consistently, we found that the upland-specific SNP3-C allele has been fixed in upland rice and is associated with tiller reduction in both natural and segregating populations (Tables 1–3). Compared with SNP3-T allele, the SNP3-C allele is associated with lower expression of *OsTb2*^{3bp+}

under both rainfed upland and irrigated conditions (Fig. 6). Our transgenic data and field experiments based on inbred rice lines both showed that the expression of *OsTb2* positively regulates tiller number, as opposed to the function of *OsTb1*. So, we concluded that the C-type SNP in the 3'-UTR of *OsTb2* is a causal mutation that confers the adaptive fewer tillers in upland rice and was fixed by artificial selection during dryland adaptation.

It should be mentioned that in a growth season in 2017 where our upland field experienced an extreme drought, we observed an unexpected induction of *OsTb2* expression associated with the C-type allele (Supplementary Fig. 9), contrary to what was observed in the irrigated field in that same growth season as well as what we observe in both irrigated and upland fields in this growth season of 2019, we reasoned that it was because the drought stress was so extreme that another feedback pathway might be triggered to compensate the over-suppression of tillering. The detailed mechanism of how C-allele was dramatically induced under extreme drought remains to be elucidated by future studies; this could represent another unknown regulatory pathway. Interestingly, in our association analyses in segregating populations (Tables 2, 3), we repeatedly observed the significant association between SNP3 and tiller number from 40 DAG, but the association between *indel*-I and tiller numbers only got significant from 50 DAG. The detailed mechanism for this fact is not clear, but given that *OsTb2* has a much higher expression in 40 DAG than in 50 DAG (supplementary Fig. 5), it is very likely that in 40 DAG the effect of gene expression variation caused by SNP3 masks the effect of protein activity difference caused by *Indel*-I.

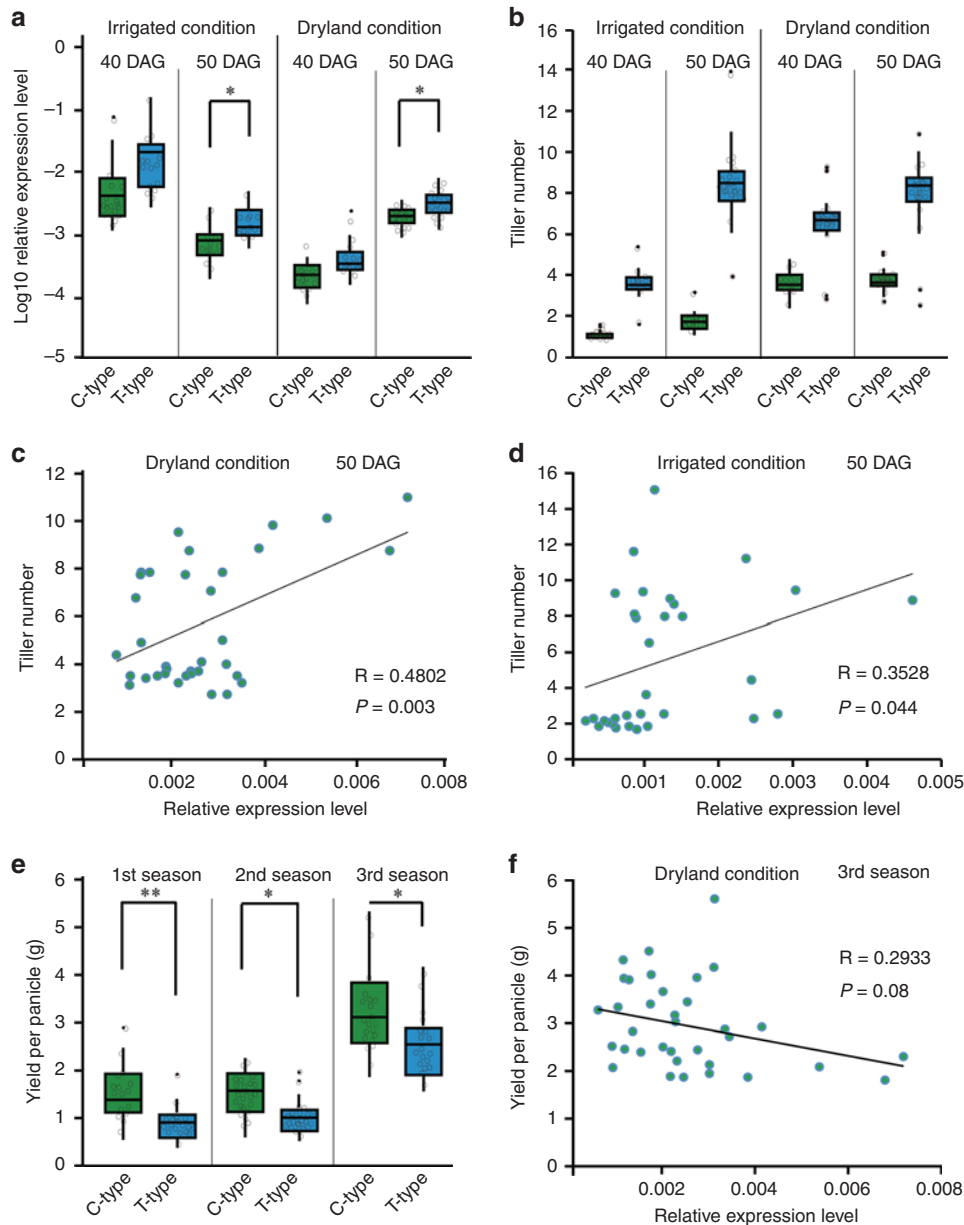


Fig. 6 *SNP3* is associated with *OsTb2* gene expression and phenotypes. **a** For the 39 cultivars, C-type cultivars have lower *OsTb2* expression than the T-type at 40 DAG and 50 DAG under both irrigated and dryland conditions. **b** C-type is associated with fewer tillers under irrigated and dryland conditions. The expression of *OsTb2* is significantly positively correlated with tiller numbers in the 39 cultivars at 50 DAG under dryland (**c**) and irrigated (**d**) conditions. **e** C-type cultivars have significant higher yield per panicle than T-type cultivars in three growth seasons under dryland conditions. **f** The expression of *OsTb2* is negatively correlated with grain yield per panicle in the 39 cultivars in the 3rd season under dryland condition. ‘R’ refers to Pearson product-moment correlation coefficient; ‘P’ is P-value. Student’s t-test analysis indicated a significant difference (* $P < 0.05$, ** $P < 0.01$). Each dot in a, b and e represents the mean value of about 8 plants and $n > 15$ cultivars for statistics.

So far there have been quite a few genes known to control the tiller formation in rice, such as *MOC1*^{30–32}, *SPL* genes^{33,34}, *miR156*³⁵, *LB4D*³⁶, *DWARF10*³⁷, *D14*¹⁶, *D53*³⁸, *RCN8/9*³⁹, and *OsTb1*⁴⁰. Some of these genes have strong effects on rice tillering. However, to our knowledge, *OsTb2* is the only gene regulating tiller number in rice determined to have been subjected to artificial selection. The reason that *OsTb2*, rather than other genes, was selected during upland rice adaptation remains elusive. It might have been a chance occurrence. Alternatively, artificial selection may have preferred to act on *Tb1* homologues, given that they have contributed to morphological evolution across different cereal crops. This situation may have arisen because this family of genes can be easily modulated for

phenotypic evolution without a considerable detriment to other agronomic traits. This question remains to be further explored. It should be mentioned that, as a regulatory gene, the effects of *OsTb2* on tillering seems to be moderate or even minor in some conditions, because the effect sizes of the two variants (Indel 1 and *SNP3*) range from 0.47 to 2.77 in the segregating populations (Table 2, Table 3, Supplementary Table 1) and the phenotypes of the transgenic lines are significant but not dramatic (Fig. 3). But selection genes do not have to be large-effect genes. For example, a recent work reported that a minor-effect gene controlling seed dormancy was parallel selected in the domestication of soybean, rice and tomato⁴¹. The large-effect genes, such as *MOC1*, might cause too severe phenotypes that are not

suitable for agricultural production, and consequently are not favored by human selection.

Strigolactone (SLs) signalling and biosynthesis are involved in the regulation of branching in plants^{42,43}. The *D14* gene functions in the MAX/RMS/D pathway of SL biosynthesis^{16,42}. It was previously reported that *OsTb1* regulates tiller development in rice by modulating *D14* expression indirectly¹⁷; we now report that *OsTb2* can interact with *OsTb1* and may regulate *D14* expression indirectly by counteracting *OsTb1*. Consequently, *OsTb2* may be involved in balancing the *D14*-mediated SL signalling pathway. Recent studies indicate that TCPs in *Oryza sativa* (rice), *Sorghum bicolor*, and *Arabidopsis thaliana* act downstream of the auxin and MORE AUXILIARY GROWTH (MAX) pathways^{44–46,40}. Additional studies are needed to understand whether the regulation of tiller number by *OsTb2* is also associated with auxin pathways.

Evolutionary novelties often originate from gene duplication. In this study, we found that *OsTb2*, as a duplicate gene of *OsTb1*, does not function as a tiller inhibitor but evolved a function opposite that of *OsTb1*, adding an example to the classical concept of neo-functionalization^{15,47–50}. There was actually a similar report that detailed the interaction between two isoforms of an important BRANCHED1 (BRC1) transcription factor in potato⁵¹. In that case, the regular long form inhibits lateral branching, similar to BRC1 in other species, but a modified protein that originates from alternative BRC1 splicing inhibits the long form and promotes lateral branching⁵¹. In our study, two *Tb1* homologues, *OsTb1* and *OsTb2*, were shown to have antagonistic effects on rice tiller number, similar to the model of the regulation of lateral branching in potato by BRC1 isoforms and the regulation of flowering time in beets that is controlled by the interplay of two paralogs of the *Arabidopsis* FLOWERING LOCUS T (*FT*) gene with antagonistic functions⁵².

While the Mayans had a lucky break discovering plants with the *Tb1* transposon⁵¹, we are now on the cusp of understanding TCP genes and plant branching. In this context, there is the prospect that regulating *OsTb2* or other *Tb1* homologues will lead to superior outcomes in the adaptation and breeding of rice and other cereal crops.

Methods

Plant materials and phenotyping. The 84 upland and 82 irrigated accessions included in this study were collected from different regions worldwide (Supplementary Data 1). One 134 F₈ recombinant inbred lines (RILs) were generated from F₂ plants that were obtained by crossing the upland variety IRAT104 and the irrigated variety IR64. We identified RIL116, which was heterozygous for both Indel I and SNP3, and selfed this individual to produce a near-isogenic F₂ population segregating for both Indel I and SNP3. The derived near-isogenic F₂ population included 451 individuals, all of which were grown to be phenotyped and genotyped.

Phenotyping was performed in both irrigated and dryland conditions (i.e., preventing soil submergence in water to simulate a rainfed upland environment) for three growth seasons at Xishuangbanna, Yunnan province (1st season refers to the second season of 2015; 2nd season refers to the second season of 2017; 3rd season refers to the first season of 2019). For the irrigated condition, seeds were germinated in a seedbed, and seedlings were then transplanted to a paddy field, where water was ponded on the soil surface throughout the growth and developmental period. For the rainfed upland condition, we conducted direct seeding by dibbling seeds in dry soil. To fully simulate rainfed conditions, no irrigation was applied in the upland condition. When rain came, we drained any excess water to prevent soil submergence. For each accession, we planted three replicates and each replicate have 12 individuals in two rows (6 individuals in each row), with a row spacing of 30 centimetres and a plant spacing of 20 centimetres. For each line, approximately eight individuals were randomly selected and phenotyped. The tiller numbers of the accessions and RILs were surveyed at 40 and 50 DAG, and yield per panicle of the accessions were investigated. The soil water content of dryland was measured by soil moisture meters (TZS-W, Zhejiang Top Instrument Co.Ltd) at 40 and 50 DAG.

Identification of *OsTb2* using a population genetic approach. *OsTb2* was reported from our previous work¹⁰. We performed a whole-genome scan for genes

with the top *F*_{ST} and XP-CLR signals. We first determined the allele frequencies of the SNP alleles in the upland and irrigated *japonica* populations (Supplementary Data 1) using the resequencing data reported in our previous work¹⁰. Then based on the allele frequencies, we calculated the *F*_{ST} value between upland and irrigated populations using the method described by Nei⁵³. In the genome scan, we used 20-kb sliding windows with 2-kb sliding step. The *F*_{ST} value for each window was obtained by averaging the *F*_{ST} values over SNP sites in that window. To calculate the XP-CLR score, we used the software XP-CLR⁵⁴ and allele frequencies from upland and irrigated populations. A window size of 0.1 cM, a 2-kb grid size and a maximum SNP number of 150 for each window was used. *OsTb2* was found to be located in regions with the top 5% *F*_{ST} and XP-CLR signals between upland *japonica* and irrigated *japonica* accessions, which have significantly different tillering abilities¹⁰. When running the BLAST program against the rice genome using the maize *Tb1* gene sequence, the orthologue *OsTb1* has the highest identity and the paralogue *OsTb2* has the second highest identity. To further substantiate *OsTb2* is a paralogue, we downloaded maize and rice genes in this family from the Panther gene family database and use the MUSCLE software to infer the phylogenetic relationship among these genes (Supplementary Fig. 10)⁵⁵. We also used the MCscan software to do synteny analysis (Supplementary Fig. 11)⁵⁶. Our results supported that *OsTb2* is a paralogue rather than an orthologue of the maize *Tb1* gene.

Evolutionary analyses detecting *OsTb2* as under selection. For allele frequency spectrum (AFS) analysis, we resequenced the upland and irrigated *japonica* accessions at higher depth of about 15× for more accurate allele frequency estimation. Using the SNP information around the *OsTb2* gene region (from 80 kb downstream to 80 kb upstream) and *indica* rice as outgroup, we generated the derived AFSs for SNPs from windows, which are 10 kb, 20 kb, ..., and 80 kb away from the putative causal mutations of the *OsTb2* gene for both upland and irrigated rice populations and then checked if the AFSs display a U-shape pattern, a signal of the hitch-hiking effect. The raw reads that map this gene region can be provided upon request. We further used a nonparametric test (Kolmogorov-Smirnov test) to examine if the U-shape pattern decays with the increasing distance from the focal mutation.

We applied the Hudson-Kreitman-Aguadé (HKA)⁵⁷ and population branch statistic (PBS)⁵⁸ to identify candidate genes having recently reached fixation. Three populations (irrigated *japonica*, upland *japonica* and *indica*) were used to calculate pairwise *F*_{ST} values of SNPs. For all the 44,643 genes, mean *F*_{ST} were generated using SNPs only located in coding regions. Then a classical transformation by Cavalli-Sforza $T^{pop1-2} = -\log(1 - F_{ST})$ was obtained to estimate the divergence time *T* between Population1 (Pop1) and Population2 (Pop2) in units scaled by population size. The length of population branch can be obtained by Eq. 1:

$$PBS_{pop1} = (T^{pop1-2} + T^{pop1-3} + T^{pop2-3})2^{\Delta} - 1 \quad (1)$$

Then we recorded the SNPs number (*A*) of each population and the number (*B*) of fixed SNPs (the sites with *F*_{ST} > 0.9 for the population compared with both two other populations), performed the HKA test by comparing the ratio of *A/B* to the genome-wide average and testing the null hypothesis *A/B*(gene) = *A/B*(genome-wide) using a Pearson's Chi-square test on the 2 × 2 contingency table. Finally, genes with PBS value ranking genome-wide top 5% and a significant nominal *P*-value (<0.05) for the HKA test were considered as sweeps candidates. ORF evidence and notes were extracted from rice annotation database.

SweeD⁵⁹ was used for detecting selective sweeps in the upland and irrigated *japonica* populations with the following settings (–folded –grid 40000). And the regions with top 5% composite likelihood ratio statistic⁶⁰ were identified as having significant selection signatures.

Identification of variations around *OsTb2* and genotyping. DNA fragments around the *OsTb2* gene were amplified from the 130 accessions by *tb2*-up-*f*/*tb2*-up-r and *tb2*-*f*/*tb2*-r primers (Supplementary Table 2), and subjected to Sanger sequencing. Seven SNPs and two indels were identified by alignment with MEGA software.

Based on the sequence around SNP3 and Indel I, we designed dCAPS for the genotypes of these loci. For SNP3, a 124 bp fragment was amplified via PCR by *tb2*-SNP3-*f*/*tb2*-SNP3-*r* primers (Supplementary Table 2) and then cut using the restriction enzyme *B*sl I. Two bands (99 bp and 25 bp) were observed in the gel for the C-genotype, while the T-genotype could not be digested. For Indel I, 200 bp PCR products were obtained with (*tb2*-indel-gate-*f*/*tb2*-indel-*r*) primers (Supplementary Table 2) and then digested with the restriction enzyme *B*sl I. Two bands (130 bp and 70 bp) were observed in the gel for to 3bp+ genotype, while 3bp- type could not be cut.

Association analysis and conditional association analysis. Association analysis was used to test the association between SNP3, Indel I and tiller number. The genotypes of the alleles of 130 accessions were determined using Sanger sequencing, and the genotypes of the RILs of NILs were determined using dCAPS markers (Supplementary Table 2). The accessions were then classified into three different genotypes (two homozygotes and one heterozygote). Student's *t*-test was subsequently performed to compare the tillers between the two homozygous groups.

Conditional analysis: A total of 52 accessions with the T-genotype for the SNP3 site, but different Indel I genotypes were used to test the association between the Indel I genotypes and phenotypes; 50 accessions with the 3bp+ genotype for Indel I, but different genotypes for the SNP3 locus were used to assess the association between SNP3 genotypes and tiller numbers.

Quantification of gene expression using real-time PCR. We conducted quantitative PCR to survey the expression level of *OsTb2* in different genotypes including 39 cultivars (Supplementary Data 2) and 12 lines from 134 RILs according 3bp+/C and 3bp+/T genotype. Total RNA was extracted from the tiller node tissues of the plant materials at 40 DAG or 50 DAG. After digesting the RNA samples with DNase I (Fermentas), we performed reverse transcription with the Fermentas K1632 Revert Aid H minus First-Strand cDNA kit. We used SYBR-Green Supermix (Bio-Rad) to conduct real-time PCR and analysed the samples in the ABI 7000 Sequence Detection System. β -actin (actin-*f*/actin-*r*) was used as an internal control. The *OsTb2*-specific qPCR primers for the transcript included *tb2*-qPCR-*f* and *tb2*-qPCR-*r* (Supplementary Table 2).

Vector construction and genetic transformation. The coding region of *OsTb2* was amplified from rice (IRAT104 and IR64 cultivars, which were the parents of the RIL population used to identify this gene) cDNA by PCR using *Kpn* I and *Bam* H I linker primers (Supplementary Table 2). The resulting *OsTb2* fragment was inserted into the *Kpn* I and *Bam* H I sites of *pCUBi1390*⁶¹, generating *Ubipro::OsTb2*. All the vectors were introduced into *Agrobacterium tumefaciens* strain *EHA105* and then transferred into Nipponbare plants via *Agrobacterium*-mediated callus transformation⁶². Phenotyping of the T₂ transgenic lines was performed using the above methods at 25 DAG to 73 DAG.

Subcellular localization of GFP-*OsTb2* fusion proteins. The open reading frames (ORFs) of *OsTb2* were inserted into *pMDC43* as C-terminal fusions with the green fluorescent protein (GFP) reporter gene driven by the CaMV 35 s promoter⁶³. These constructs were transformed into the leaves of 3-week-old tobacco (*Nicotiana benthamiana*) by *A. tumefaciens* infiltration⁶⁴. DAPI staining was used to identify the nucleus. The resulting green fluorescence of protoplasts expressing GFP-*OsTb2* was observed using a confocal laser-scanning microscope (LSM700, Zeiss, Jena, Germany).

Bimolecular fluorescence complementation assay. Complementary DNAs of *OsTb2* and *OsTb1* were cloned into the bimolecular fluorescence complementation (BiFC) vectors *pnYFP-X* and *pcCFP-X*, respectively, with GUS also cloned as a negative control. The constructs were cotransformed into *Nicotiana benthamiana* protoplasts for transient expression. Protoplast isolation from tobacco leaf tissues and PEG-mediated transformation were performed according to Bart et al.⁶⁵. Cells were incubated at 28 °C in the dark overnight. A confocal laser-scanning microscope (LSM700, Zeiss, Jena, Germany) was used to observe the green fluorescence of protoplasts. The 35S::GFP construct and AHL22 were used as a control and a nuclear marker protein, respectively⁶⁶.

Protein coimmunoprecipitation assay. The recombinant constructs *GFP-OsTb2* and *MYC-OsTb1* were introduced into rice protoplasts, and protein extracts were prepared as described by He⁶⁷. The protein extracts were precipitated with anti-GFP agarose beads (CMC Scientific, <http://www.cmcscientific.com>) overnight. Then, proteins bound to the beads were resolved by SDS-PAGE and detected by Western blotting using anti-GFP (dilution at 1:1000; ab1218, abcam), anti-MYC (dilution at 1:1000; ab264433, abcam) primary antibodies (MBL, <http://www.mblintl.com/>) and HRP-labelled goat anti-mouse secondary antibody (dilution at 1:5000; ab97023, abcam).

Transient expression assays in rice protoplasts. For the *D14* promoter repression assay, two forms of *OsTb2* were used in the system. The full-length *OsTb2* cDNAs were fused into the *pRTVcMyc* vector, driven by the 35 s promoter, to generate *pRTVcMyc-OsTb2^{3bp+}* and *pRTVcMyc-OsTb2^{3bp-}*. To generate the *D14pro::LUC* reporter gene, the *D14* promoter (*D14pro*) was amplified. The plasmid carrying the GUS gene under the control of the 35 s promoter was used as a normalization control. The presented values represent the means \pm s.d. of six technical replicates. Cotransformation of the *D14pro::LUC* reporter and *pRTVcMyc-OsTb2^{3bp+}* or *pRTVcMyc-OsTb2^{3bp-}* was performed according to He et al.⁶⁷ to identify the effect of *OsTb2* in the transient assay. The *Renilla* luciferase reporter gene (*REN*) under the control of CaMV35S promoter was used as an internal control to normalize the data for eliminating variations in the experiment.

Dual-luciferase assays in tobacco leaves. The effector plasmids *pMDC43-OsTb2*, *pMDC43-OsTb1*, and *pMDC43-OsMADS57* were cloned as described above. The reporter plasmid *pGreen-D14pro-LUC* encodes two luciferases, firefly luciferase controlled by the *D14* promoter and the *Renilla* luciferase controlled by the constitutive 35 s promoter. The *D14pro*, fused to the minimum 35 s promoter, was PCR amplified from the 35 s template and cloned into the Hind III/*Bam* HI sites of the vector *pGreen-0800-LUC*. *pGreen-D14pro-LUC* was transformed into

Agrobacterium (strain *EHA105*) carrying the helper plasmid *pSoup-P19*, which also encodes a repressor of co-suppression⁶⁸. The *Agrobacterium* strain containing both the reporter *pGreen-D14pro-LUC* and the helper *pSoup-P19* was used either alone or mixed with the *Agrobacterium* strain containing the effector plasmids *pMDC43-OsTb2*, *pMDC43-OsTb1*, and *pMDC43-OsMADS57*, as shown in Fig. 4b. *pMDC43-OsGRF4* was used as a negative control effector. Overnight cultures of *Agrobacterium* were collected by centrifugation resuspended, and infiltrated as described above⁶². After 3 days, using commercial Dual-LUC reaction (DLR) reagents according to the manufacturer's instructions (Promega) leaf samples were collected for the Dual-LUC assay. Specifically, we excised leaf discs from the site (ca. 1–2 cm in diameter) of *Agrobacterium* infection, ground using liquid nitrogen, and homogenized using 100 μ l of Passive Lysis buffer (Promega). Then, we mixed 20 μ l of the crude extract with 100 μ l of Luciferase Assay buffer (Promega), and examined the firefly luciferase activity (LUC) using a luminometer (BG-1, GEM Bio-medical Inc). After the measurement of firefly luciferase activity, 100 μ l of Stop and Glow buffer (Promega) was added to quench the firefly luciferase and initiate the *Renilla* luciferase reaction.

Yeast one-hybrid assay using the pLacZi2u/pB42AD system. We followed the previous reported procedure⁶⁹. Briefly, the coding sequence of *OsTb2* was inserted into the MCS of *pB42AD* to generate an AD-fusion construct (*pB42AD-OsTb2*), and *D14pro* was inserted into the MCS of the *pLacZi2u* reporter plasmid (*pLacZi2u-D14pro*). The *pB42AD-OsTb2* plasmid was cotransformed with *pLacZi2u-D14pro*, including the *LacZ* reporter gene driven by a *D14pro* fragment, for testing in *EGY48* yeast strain. Transformants were grown on SD (galactose + raffinose)/-Ura/-Trp/X-gal plates.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Data supporting the findings of this work are available within the paper and its Supplementary Information files. A reporting summary for this Article is available as a Supplementary Information file. The datasets generated and analyzed during the current study are available from the corresponding author upon request. DNA-seq data were deposited in the National Center for Biotechnology Information (NCBI) under the SRA accession number [PRJNA595072](https://www.ncbi.nlm.nih.gov/sra/PRJNA595072). The source data underlying Fig. 5b as well as Tables 1, 2, and 3 are provided as a Source Data file.

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Author contributions

F.Y.H., J.L. and W.W. conceived the project. J.L., L.Y.H. and Y.S.Z. designed and performed the experiments. Shila.Z., G.F.H., J.Z., Y.C.B., M.N. and Q.F. performed the genotyping and phenotyping analysis. W.M.H., Shila.Z., P.Z., Y.Z., Shile.Z. and H.C. performed the data analysis. J.L. and L.Y.H. wrote the manuscript, with L.J.W. revising the draft for submission and guiding the responses to referees and correction of the final manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare no competing interests.

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An innovated crop management scheme for perennial rice cropping system and its impacts on sustainable rice production

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ABSTRACT

Perennial grain has been proposed to provide an effective means of ensuring both food and ecological security. The newly released cultivar of perennial rice 23 (PR23) represents a new rice production system that is based on no-tillage. Nevertheless, how perennial rice responds to this new system remains unclear. Two field experiments were conducted over four successive seasons from 2016 to 2017 in Jinghong, Yunnan Province, Southern China. Field experiment 1 showed perennial rice is an economically viable and environmentally safe cropping system compared to annual rice, and could obtain a stable and sustainable grain yield economically for successive seasons across years. In the perennial rice cropping system, N fertilizer had some negative effects on the regrowth of perennial rice. Field experiment 2 with four N rates N0, N1, N2 and N3 with 0, 120, 180 and 240 kg N ha⁻¹, respectively and three planting densities D1, D2 and D3 with 10, 16.7 and 22.6 plants m⁻², respectively on perennial rice was conducted to assess and ameliorate these negative effects of N fertilizer on the regrowth of perennial rice. The results showed that: (1) the N2D3 treatment (180 kg N ha⁻¹ integrated with 22.6 plants m⁻²) resulted in a stable and high grain yield across three successive regrowth seasons (6.93 t ha⁻¹) and optimized yield components (panicle no. m⁻², spikelet no. panicle⁻¹, grain weight) and root activity (10.81 g h⁻¹ m⁻²); (2) the regrowth of perennial rice 23 was significantly limited by N fertilizer ($P < 0.05$), and the N0D2 treatment had the best regrowth ability (97.8 %) across the three regrowth seasons; (3) additionally, the N2D3 treatment had the best N net productivity (27 kg N kg⁻¹), profit (79 CNY kg⁻¹) and sustainable production capacity (0.59), and could obtain more economic profit in successive perennial rice production. Perennial rice was able to be sustainably and economically produced for successive regrowth seasons across years, and the N2D3 treatment provided optimal conditions, which enhanced the regrowth rate, N productivity, economic benefit and yield potential. The use of less chemical N fertilizer and a higher planting density could enhance the sustainability of the grain yield and reduce fertilizer loss via a novel crop management scheme for perennial rice.

1. Introduction

Compared with the current global cropping acreage, a million more hectares of land need to be converted to crop production to meet the growing demand for food (Naylor et al., 2007). Annual crop production, which is responsible for 80 % of global food, leads to increased carbon emission, soil erosion, and water and environment pollution and requires a large amount of labour (Pimentel et al., 2012; Cox et al., 2010). Moreover, global climate change poses a high risk for annual crop yield

losses (Wan, 2018). How to sustainably meet the food demand is a current hot topic of research (Cui et al., 2018; Glover et al., 2010; Tilman et al., 2011; Pimentel et al., 2012). Significant improvements in genetics or new crop species, such as transformation from annuals to perennials, potentially provide efficient strategies to increase crop production in an environmentally sustainable way (Wan, 2018; Glover et al., 2010; Hu et al., 2003).

After sowing and transplanting, perennial crops can survive and be harvested several times in successive years (Glover et al., 2010). Indeed,

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such crops can ratoon and regrow without sowing or planting after their first year. Once perennial crops become a feasible option, farmers can reduce some production efforts, decreasing the need for and intensity of labour and increasing economic profits (Huang et al., 2018). Moreover, without plowing every year or season, the continuous lack of tillage for perennial crops would reduce soil erosion and protect arable land (Cox et al., 2006; Zhang et al., 2011). In 2010, scientists from more than ten countries revealed that perennial crops would provide an effective means of protecting crop yields and the environment (Glover et al., 2010) and indicated that perennial crops would be economically viable within 20 years.

In 2018, the first cultivar of perennial rice 23, named PR23 (No. 2018033, <http://www.ricedata.cn/variety/varis/618801.htm>), which was bred via the clonal propagation characteristics of the rhizome of *Oryza longistaminata* and is capable of surviving for consecutive years, was released in China (Huang et al., 2018; Zhang et al., 2017, 2019c). PR23 was obtained from the cross between *Oryza sativa* cv. RD23 and *O. longistaminata*. RD23 is a popular *Indica* lowland rice cultivar from Thailand, and is grown widely across south-east Asia because of its broad adaptation, high yield potential, good disease resistance, and high grain quality. In contrast, *O. longistaminata* is a wild rhizomatous perennial species with poor agronomic characteristics which is original from Africa. The cross between the two species was made in 1997 to combine the perennial habit of *O. longistaminata* with the agronomic features, broad adaptation (Tao and Sripichitt, 2000), and yield potential of RD23 via iterative segregating populations from F₂ in 2003 to F₁₀ in 2010 (Huang et al., 2018).

The cultivar PR23 is a breakthrough as it represents a turning point from annual to perennial in crop domestication and improvement. Without the need for plowing, seeding, and transplanting during successive regrowth seasons, perennial rice can reduce soil erosion and the need for intensive labour and input in fields (Huang et al., 2018). To date, the perennial rice trail is on the way in China, Myanmar, Laos, Cambodia, Thailand, Vietnam, Indonesia, Uganda and Cote d'Ivoire via International Perennial Rice Collaboration organized by Yunnan University. In China, perennial rice has been tested in more than 10 provinces (Yunnan, Guangxi, Guangdong, Fujian, Hunan, Hubei, Henan, Zhejiang, Jiangxi and Guizhou) and over an area greater than 5000 ha as of 2019.

Previous research on perennial rice has demonstrated that it can be widely planted in South China and Laos (Zhang et al., 2017; Huang et al., 2018), enhance the profits of farmers and reduce labour in fields (Huang et al., 2018). However, the management of perennial rice, as well as its response to N fertilizer, remains unclear. It still needs to be determined how to offset the negative effects of N fertilizer on the regrowth of perennial rice and to maintain an appropriate perennial rice population to obtain a stable and high grain yield as well as sustainable production over years. Therefore, two experiments were conducted in this study. Experiment 1 (comparison of perennial and annual rice cropping system) was to evaluate the sustainable production ability and economic benefit of perennial rice cropping system. A field experiment (Experiment 2) using different N fertilizer rates and planting densities of perennial rice was employed to optimize crop management and the response of perennial rice in Jinghong, Yunnan Province, China, to explore the response of perennial rice to N fertilizer and planting density. Our objectives were to select the appropriate N fertilizer rate and planting density for sustainable production of perennial rice, and the results provide a theoretical indication for the sustainable production of perennial rice. Lastly, our findings provide insight into the production of perennial grains.

2. Materials and methods

2.1. Experimental site

This experiment was conducted at the Perennial Rice Research

Station of Yunnan University, Gasa town (N 20°57'22", E 100°45'43", altitude 555 m), Jinghong, Yunnan Province, China. The station is located in southern China, which has a tropical monsoon climate, and rice is harvested twice a year in this region. The average annual rainfall and temperature were 1136.6 mm and 23.3°C, respectively, and most rainfall was from April to October.

Before the experiment, regular annual rice production had been conducted in the trial field. The soil conditions are shown in detail in Table 1.

2.2. Experimental design and performance

2.2.1. Experiment 1: perennial Vs annual rice

A randomized complete blocks design with three replicates was performed over four successive seasons from 2016 to 2017. Two rice varieties were selected, perennial rice 23 (PR23) and annual rice HXR7. PR23 is a perennial rice cultivar released by Yunnan Crop Committee in 2018. HXR7 is a locally popular *Indica* lowland rice cultivar grown widely by farmers in Yunnan Province due to its high grain yield and its exceptional grain quality. The sowing and transplanting date of both HXR7 and PR23 in the first transplanting season were 30, Jan 2016 and 5, Mar 2016, respectively. In the regrowth seasons (2016S, 2017F, 2017S), the annual rice and perennial rice were managed according to the local rice production. After harvest, the crop management in annual rice consisted of plowing, reseeding and transplanting. For perennial rice, the new tillers that emerged from the rhizome of the straw were only maintained for successive regrowth seasons. After harvest, the straw was cut back 5–10 cm above the ground to maintain the uniformity of new tillers arising from rhizomes and to depress tillers from the stem. Meanwhile, no tilling was conducted across the three successive regrowth seasons. Other crop management was the same as local rice production.

2.2.2. Experiment 2: N rate and planting density experiment of perennial rice

The experiment employed a split-plot design with three replicates and was performed over four successive seasons from 2016 to 2017. There were four N fertilizer rates (0 kg N ha⁻¹ (N0), 120 kg N ha⁻¹ (N1), 180 kg N ha⁻¹ (N2) and 240 kg N ha⁻¹ (N3)) used in the main plots and three planting densities (10 plants m⁻² (D1), 16.7 plants m⁻² (D2) and 22.6 plants m⁻² (D3)) among subplots 20 m² in size. These four N fertilizer rates and three planting densities generated 12 N fertilizer rates with planting density treatments: N0D1, N0D2, N0D3, N1D1, N1D2, N1D3, N2D1, N2D2, N2D3, N3D1, N3D2 and N3D3 (Tables 2 & 3).

The cultivar perennial rice 23 was sown on 15 Dec 2015 and was transplanted in a plowed and level field on 30 Jan 2016. For different rates of N application, N fertilizer (urea) was manually and evenly spread at a ratio of 5:2:2:1 during four stages corresponding to the transplanting time for 2016F or new tillers emerging, tilling, heading and filling, respectively. For different planting densities, the plant and row spacings for D1 were 27 cm and 37 cm, respectively. For D2, the plant and row spacings were 20 cm and 30 cm, respectively; for D3, the plant and row spacings were 17 cm and 26 cm. The crop management of perennial rice was the same with Experiment 1.

Table 1

Soil conditions prior to the initiation of experiments.

Soil layer (cm)	pH	SOM (g kg ⁻¹)	TN (g kg ⁻¹)	AN (mg kg ⁻¹)	AP (mg kg ⁻¹)	AK (mg kg ⁻¹)
0–20	5.05	34	2.1	155.6	7.58	139.1

SOM: soil organic matter, TN: total nitrogen, AN: available nitrogen, AP: available phosphorus, AK: available potassium.

Table 2
Parameters of the different treatments.

Treatment	Details N rates (kg ha ⁻¹)	Plants (m ⁻²)
N0	0	–
N1	120	–
N2	180	–
N3	240	–
D1	–	10
D2	–	16.7
D3	–	22.6
N0D1	0	10
N0D2	0	16.7
N0D3	0	22.6
N1D1	120	10
N1D2	120	16.7
N1D3	120	22.6
N2D1	180	10
N2D2	180	16.7
N2D3	180	22.6
N3D1	240	10
N3D2	240	16.7
N3D3	240	22.6

Table 3
Dates of sowing, transplanting, cutting back and harvesting of perennial rice over four seasons during 2016–2017.

Season	Date			
	Sowing	Transplanting	Cutting back	Harvest
First season (2016F)	15, Dec 2015	30, Jan 2016		8, Jun 2016
Second season (2016S)			10, Jun 2016	18, Oct 2016
Third season (2017F)			17, Feb 2017	18, Jun 2017
Fourth season (2017S)			19, Jun 2017	28, Oct 2017

2.3. Measurements

2.3.1. Grain yield and sustainable yield index

In each plot, perennial rice was manually harvested from an area greater than 5 m² at harvest time and was adjusted to a 14 % water content (the international standard) to measure grain yield. The sustainable yield index (Muhammad et al., 2020) was used to evaluate the sustainable production capacity of perennial rice.

$$\text{Sustainable yield index (SYI)} = (\text{Ymean} - \sigma) / \text{Ymax} \quad (1)$$

Where Ymean is the mean grain yield of a treatment over four seasons, σ is treatment standard deviation over four seasons, and Ymax is the maximum grain yield of a treatment over four seasons.

2.3.2. Yield components

At harvest time, three replications with 10 uniform plants which could represent the rice population were selected to measure the yield components of perennial rice in each plot. Yield components of perennial rice including panicle no. m⁻², spikelet no. panicle⁻¹, grain weight and seed setting rate. The panicle no. was counted and calculated by the formula:

$$\text{Panicle no. m}^{-2} = \text{average panicle no. per plant} \times \text{planting density} \quad (2)$$

Thirty panicles were randomly selected and the number of spikelets was counted. Seed setting rate and grain weight was measured by floating selection and oven drying method. All the sample grains were watered for 3 min, floated to separate empty from filled grains, and these two fractions were then weighed. 3 g empty grains and 30 g filled grains

were selected with three replications, and then dried to stable weight and counted the number to calculate the grain weight and seed setting rate by the formulae:

$$\text{Grain weight (mg)} = \text{filled grain weight} / \text{filled grain no.} \quad (3)$$

$$\text{Seed setting rate (\%)} = \text{filled grain no.} / (\text{empty grain no.} + \text{filled grain no.}) \times 100 \% \quad (4)$$

2.3.3. Regrowth rate

In the first season of 2016 (2016F: transplanting season), we set the regrowth rate to 100 %. In the following regrowth seasons, the second season in 2016 (2016S), first season in 2017 (2017F) and second season in 2017 (2017S), the regrowth rate was measured 7–10 days after cutting back perennial rice. In each subplot, all plants were used to calculate the regrowth rate during each regrowth season.

2.3.4. Root activity

Root activity was measured by bleeding sap. At 19:00 after sunset, three uniform plants were selected and cut 7–10 cm above the ground (Song et al., 2011). These plants were then covered by weighted cotton wool, wrapped in plastic and bound by a rubber band in each plot. At 7:00 before sunrise the following day, cotton wool was weighted to calculate the amount of sap that had bled.

2.3.5. N productivity and profit

The N productivity, net N productivity and N profit were calculated using the following formulae:

$$\text{N productivity (kg N kg}^{-1}\text{)} = \text{grain yield in } N_i / N_i \text{ application rate} \quad (5)$$

$$\text{N net productivity (kg N kg}^{-1}\text{)} = \text{grain yield (} N_i - N_0 \text{)} / N_i \text{ application rate} \quad (6)$$

$$\text{N profit (CNY kg}^{-1}\text{)} = \text{profit (} N_i - N_0 \text{)} / N_i \text{ application rate} \quad (7)$$

Note: N_i is the N rate, where i ≥ 1.

2.4. Statistical analysis

Split-plot analysis with three-way ANOVA (N rate and planting density were set as two fixed factors, and season was set as a random factor) was used to assess differences of the significance of the main plot and subplot and interactions of the treatments. When the three-factor or two-factor interaction effects were significant, single factor effects were analysed. If single factor effects were significant, one-way ANOVA was used to compare the effects of the different seasons or N treatments or planting densities on the measured variables with three replications. F-tests were conducted, and multiple comparisons were performed using the least significant difference test (LSD) (P ≤ 0.05). Experimental data was analysed with the IBM SPSS statistical package v.20.0 (SPSS, Inc., Chicago, IL, USA), and the figures were generated using Origin 2015 (Sys Software, Inc.).

3. Results

3.1. Perennial vs annual rice

In the experiment 1 of 2016–2017, perennial rice (6.46 t ha⁻¹) showed not significantly but consistently higher grain yield in 4 seasons (Fig. 1a), which was 3.8 % higher than annual rice (6.22 t ha⁻¹). Both annual and perennial rice had robust sustainable production ability (more than 0.80) (Fig. 1b), the SYI of perennial rice (0.80) was a bit less than annual rice (0.82).

For the economic benefit, perennial rice was significantly superior to annual rice (Fig. 2). In the transplanting season (2016F), the input of annual and perennial rice cropping system was on the same level

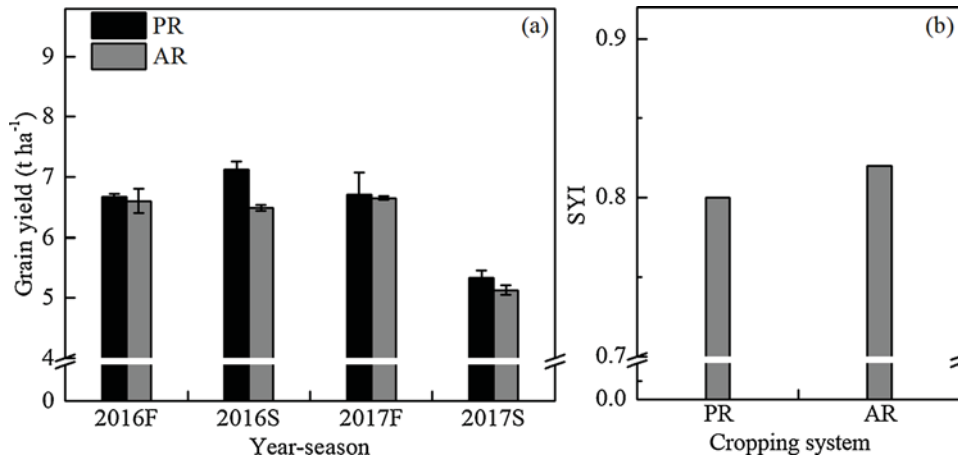


Fig. 1. The grain yield and sustainable yield index (SYI) of perennial rice (PR) and annual rice (AR) cropping system in the experiment 1. (a) Grain yield of perennial and annual rice. (b) Sustainable yield index of perennial and annual rice. Error bars are the standard errors (SE). Bars with different letters were significantly different. 2016F, first rice season of 2016. 2016S, second rice season of 2016. 2017F, first rice season of 2017. 2017S, second rice season of 2017.

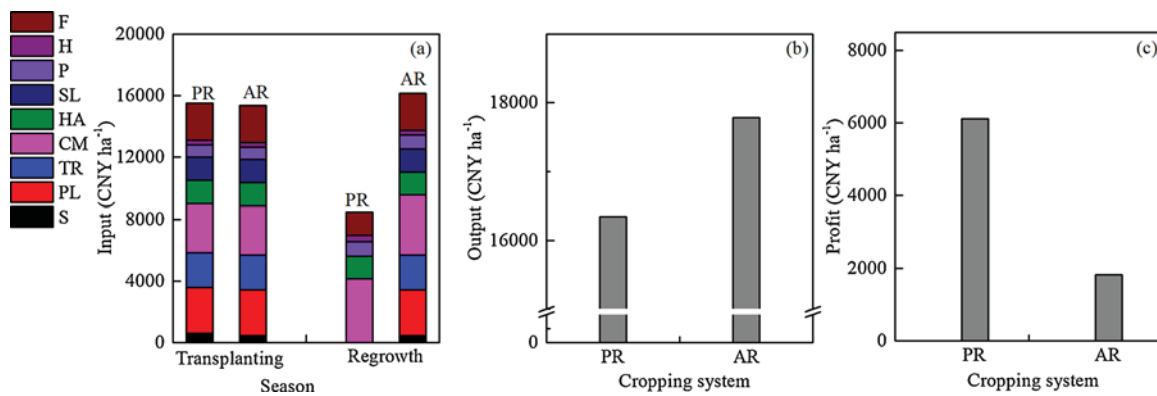


Fig. 2. The input, output and profit of perennial (PR) and annual rice (AR) cropping system in experiment 1. (a) Input of PR and AR cropping system. The total input including: F, fertilizer. H, herbicide. P, pesticide. CM, crop management. HA, harvest. TR, transplanting. PL, plowing. SL, seedling. S, seeds. (b) Output of PR and AR cropping system. (c) Profit of PR and AR cropping system.

(Fig. 2a), with 15,362 and 15,512 CNY ha⁻¹, respectively, while in the regrowth seasons, without seeds, seedling, plowing and transplanting, perennial rice economized 7684 CNY ha⁻¹ each season than annual rice cropping system. Although the output of annual rice cropping system was 8.8 % higher than perennial rice (Fig. 2b), the profit of perennial rice (6114 CNY ha⁻¹) was significantly higher (235 %) than annual rice (1827 CNY ha⁻¹) (Fig. 2c). The perennial rice cropping system has sustainable and stable production ability but would be more economic when compared to annual rice.

3.2. Grain yield and sustainable production capacity

The grain yield of perennial rice over four successive seasons from field experiment 2 is shown in Fig. 3. In the first season (2016F: transplanting season), the grain yield was high, and N2D3 resulted in the highest grain yield (9.93 t ha⁻¹). Despite the transplanting season (2016F), the grain yield remained stable across three successive regrowth seasons (Table 4). The grain yield was determined by the interaction of season and N rate with the planting density ($P < 0.01$) as well as either both of them and N rate ($P < 0.001$) over successive regrowth seasons (Table 4). For different N rates, N1, N2 and N3 significantly increased the grain yield compared with N0, with increases of 74 %, 159 % and 153 %, respectively. Among the different planting densities, D3 (4.96 t ha⁻¹) resulted in a significantly higher grain yield than D1 (3.91 t ha⁻¹). The N2D3 treatment significantly increased the grain yield (6.93 t ha⁻¹) relative to the other treatments in the three

successive regrowth seasons.

Fig. 4 shows the sustainable yield index of perennial rice in 4 seasons. Both high N rate (N2: 0.55 and N3: 0.57) and planting density (D3: 0.52) could significantly increase the sustainable production capacity of perennial rice. The N2D3 treatment (0.59) resulted in the highest sustainable production capacity in 4 seasons, followed by N3D2 (0.58).

3.3. Yield components

Panicle no. m⁻², spikelet no. panicle⁻¹, grain weight and seed-setting rate were the major determinants of the grain yield in the rice fields.

For the successive regrowth seasons of perennial rice, panicle no. m⁻² was significantly affected by the interaction of season and N rate with planting density ($P < 0.05$), N rate with season ($P < 0.05$), N rate ($P < 0.01$), planting density ($P < 0.01$) and season ($P < 0.05$) (Table 4). N2 (269), N3 (285) and D3 (286) showed a significantly higher panicle no. than the other N rates ($P < 0.05$) and planting densities ($P < 0.05$), and N2D3 led to the highest panicle no. m⁻² (333) (Table 4). Different from panicle no. m⁻², the interaction between season and N rate ($P < 0.01$), season and planting density ($P < 0.05$), N rate ($P < 0.001$) and planting density ($P < 0.05$) had significant effects on spikelet no. panicle⁻¹. N2 (132), N3 (131) and D1 (124) showed a significantly higher spikelet no. panicle⁻¹ than the other groups, and N3D1 (145) showed the highest spikelet no. panicle⁻¹ over successive regrowth seasons. The interaction between N rate and planting density with season significantly affected grain weight ($P < 0.001$). There was no significant difference among the

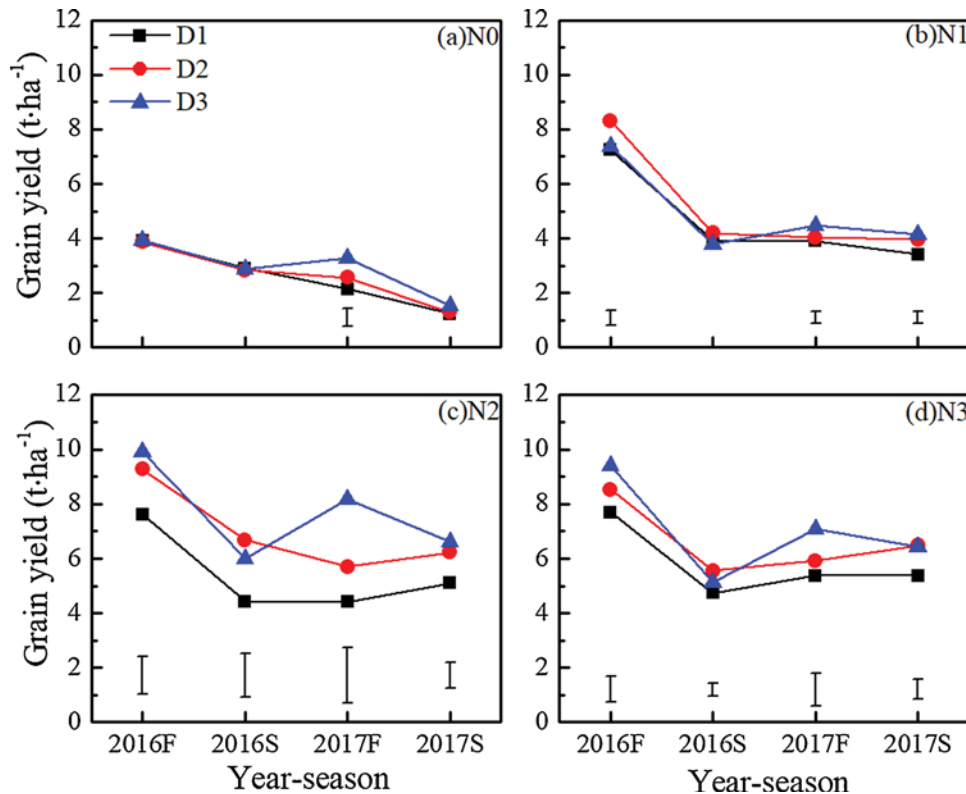


Fig. 3. Grain yield of perennial rice under different N rates and planting densities in 2016–2017. 2016F: first season in 2016 (transplanting season). 2016S: second season in 2016. 2017F: first season in 2017. 2017S: second season in 2017. Vertical bars represent the standard error for different treatments.

different N rates and planting densities ($P < 0.05$). Seed-setting rate was significantly affected by season ($P < 0.05$) and N rate ($P < 0.05$). NO level (86.34 %) led to the highest seed-setting rate compared with the other N rates, but there was no significant difference among the different planting densities. N0D3 had the best seed-setting rate at 89.92 %. The N2D3 treatment resulted in a higher grain yield through its significant effects of panicle no. m^{-2} and spikelet no. m^{-2} on the grain yield.

3.4. Regrowth rate and root activity

(1) Regrowth rate

A high regrowth rate is essential for enhancing rice populations and increasing the grain yield during successive regrowth seasons. The regrowth rate of perennial rice decreased significantly ($P < 0.05$) (Table 5), and the average regrowth rate was 90.24 % in the fourth season (2017S). In three successive regrowth seasons, the regrowth rate of perennial rice was determined by the interaction of N rate and season with planting density ($P < 0.001$) and season with planting density ($P < 0.01$) and N rate ($P < 0.001$) (Table 5). In two years, the regrowth rate declined as the N rates increased (Fig. 5), and N0 had the highest regrowth rate (97.34 % in the fourth season). The regrowth rate increased as planting density increased. D3 had the highest regrowth rate (94.11 % in the fourth season). By the fourth season, the N0D2 treatment had the highest regrowth rate (97.84 %). The N2D3 treatment also had a relatively high regrowth rate (92.18 %).

(2) Root activity

Roots are key for the absorption of soil water and nutrients; indeed, high levels of root activity provide the basis for the regrowth of perennial rice during successive regrowth seasons. Over four seasons, perennial rice showed stable root activity during regrowth seasons (Fig. 6). Root activity was significantly affected by the interactions of season and N rate with planting density ($P < 0.001$) and N rate with season ($P < 0.05$) and N rate ($P < 0.001$) and planting density ($P < 0.001$) during the regrowth seasons. N2 (9.49 $g\ h^{-1}\ m^{-2}$) and D3 (8.68 $g\ h^{-1}\ m^{-2}$) had the

highest root activity among the different N rates and planting densities, and N2D3 (10.81 $g\ h^{-1}\ m^{-2}$) had the highest root activity over the three regrowth seasons, followed by N3D3 (10.33 $g\ h^{-1}\ m^{-2}$).

4. N productivity

The N productivity of perennial rice at different N rates and plant densities on perennial rice are shown in Fig. 7. In low N fertilizer rate (N1: 41 $kg\ N\ kg^{-1}$) and high planting density (D3: 38 $kg\ N\ kg^{-1}$), the N productivity was significantly higher than high N rate and low planting density (Fig. 7a). The N1D2 and N2D3 treatments resulted in the highest values, both were 43 $kg\ N\ kg^{-1}$. Based on N0 and D1, plants could use the N fertilizer more effectively in N2 and D2, D3, the N net productivity of N2D3 showed the highest value, was 27 $kg\ N\ kg^{-1}$ (Fig. 7b). The results illustrated N2D3 treatment was the optimal scheme for N productivity of perennial rice.

4.1. Relationship between grain yield and yield components, regrowth rate and root activity

For perennial rice, N rate significantly affected grain yield, root activity and regrowth rate (Tables 4 & 5). The grain yield of perennial rice was significantly positively correlated to the root activity ($P < 0.01$) (Fig. 8a). Due to the high regrowth rate in 4 seasons (more than 90 %), the regrowth rate had a positive but not significant relationship with the grain yield ($P > 0.05$) (Fig. 8b). Despite the positive but not significant relationship of the regrowth rate with the grain yield, root activity was the main factor that affected the grain yield and other yield components of perennial rice. Indeed, the stability in root activity over four successive seasons reflects the high potential that perennial rice has to produce sustainable yields over several years.

Table 4
Yield of perennial rice over three regrowth seasons during 2016–2017.

Treatment	Grain yield (t ha ⁻¹)	Panicle no. m ⁻²	Spikelet no. panicle ⁻¹	Grain weight (mg)	Seed setting rate (%)
Season					
2016S	4.42a	217b	115a	23.80c	81.12b
2017F	4.76a	280a	113a	24.69b	80.35b
2017S	4.32a	216b	102a	25.74a	88.23a
N rate					
N0	2.29c	173c	71c	25.07a	86.34a
N1	3.99b	223b	108b	24.58a	82.67bc
N2	5.93a	269a	132a	24.82a	84.32ab
N3	5.79a	285a	131a	24.50a	79.61c
Planting density					
D1	3.91b	182c	124a	24.89a	83.72a
D2	4.61ab	244b	109b	24.49a	83.80a
D3	4.96a	286a	98b	24.85a	82.19a
ANOVA					
S(df = 2)	0.435(ns)	6.815*	1.075(ns)	4.413(ns)	14.582*
N(df = 3)	31.283***	14.057**	20.814***	1.118(ns)	5.907*
D(df = 2)	4.664(ns)	27.999**	7.954*	3.612(ns)	0.715(ns)
N × S(df = 6)	6.513**	4.129*	5.495**	0.792(ns)	1.164(ns)
D × S(df = 4)	5.677**	2.920(ns)	3.866*	0.244(ns)	1.302(ns)
N × D(df = 6)	4.698*	1.62(ns)	0.559(ns)	0.719(ns)	2.501(ns)
N × D × S(df = 12)	2.706**	2.413*	1.548(ns)	3.373***	1.708(ns)

2016S: second season in 2016. 2017F: first season in 2017. 2017S: second season in 2017.

Different letters within a column represent significant differences at $P < 0.05$ (LSD).

S: season. N: nitrogen rate. D: planting density. N × S: interaction effect between nitrogen rate and season. D × S: interaction effect between planting density and season. N × D: interaction effect between nitrogen rate and planting density. N × D × S: interaction effect between nitrogen rate, planting density and season.

*represents significance at $P < 0.05$, ** represents significance at $P < 0.01$, *** represents significance at $P < 0.001$, ns represents no significance.

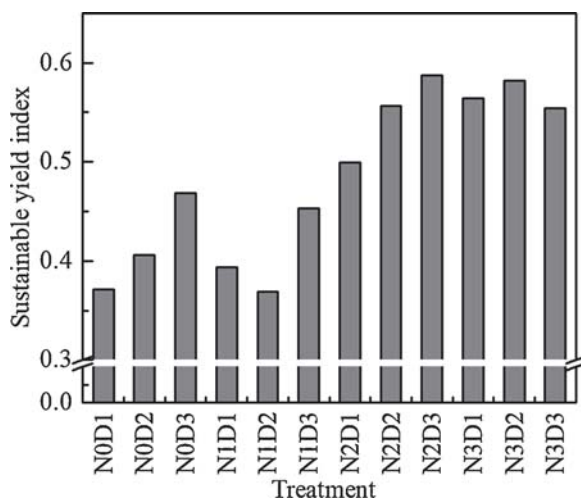


Fig. 4. The sustainable yield index of perennial rice over 4 seasons in 2016–2017.

4.2. Economic benefits and N profit

In perennial rice production, the input in transplanting season (2016F) mainly includes seeds, seedling, plowing, transplanting, crop management, pesticide and herbicide, fertilizer and harvest (Fig. 9). In the regrowth seasons (2016S, 2017F and 2017S), without seeds,

Table 5
Regrowth rate and root activity during the regrowth seasons of 2016–2017.

Treatment	Regrowth rate (%)	Root activity (g h ⁻¹ m ⁻²)
Season		
2016S	96.36a	6.907b
2017F	92.25b	8.565a
2017S	90.24c	6.709b
N rate		
N0	97.34a	4.38d
N1	92.76b	6.94c
N2	90.75b	9.49a
N3	90.95b	8.77b
Planting density		
D1	90.86b	5.84c
D2	93.88a	7.65b
D3	94.11a	8.68a
ANOVA		
S(df = 2)	5.646(ns)	6.469(ns)
N(df = 3)	20.095***	21.053***
D(df = 2)	1.965(ns)	62.985***
N × S(df = 6)	1.240(ns)	3.230*
D × S(df = 4)	8.601**	0.573(ns)
N × D(df = 6)	1.994(ns)	0.784(ns)
N × D × S(df = 12)	18.032***	3.950***

2016S: second season in 2016. 2017F: first season in 2017. 2017S: second season in 2017.

Different letters within a column represent significant differences at $P < 0.05$ (LSD).

S: season. N: N rate. D: planting density. N × S: interaction effect between N rate and season. D × S: interaction effect between planting density and season. N × D: interaction effect between N rate and planting density. N × D × S: interaction effect between N rate, planting density and season.

*represents significance at $P < 0.05$, ** represents significance at $P < 0.01$, *** represents significance at $P < 0.001$, ns represents no significance.

seedling, plowing and transplanting, the new tillers ratooned from the rhizome the input decreased 7250 CNY ha⁻¹ each season when compared to 2016F (14,917 CNY ha⁻¹). The output of perennial rice mainly was the output of grain yield, and N2D3 produced significantly higher output (23,808 CNY ha⁻¹) and economic profit (14,223 CNY ha⁻¹) in 4 seasons. Additionally, N2D3 produced significantly higher N profit (79 CNY kg⁻¹) in 4 seasons (Fig. 7c). Perennial rice had significantly lower input in regrowth seasons, N2D3 treatment produced significant economic profit and N profit, and was the most economic scheme in perennial rice production.

5. Discussion

5.1. Perennial vs annual rice

SYI is an important factor to evaluate whether a crop could produce sustainable and stable grain yields in consecutive years (Muhammad et al., 2020). The perennial rice 23 performed the same yield potential as annual rice and high SYI illustrated that perennial rice had sustainable and stable production ability and yield potential over the years. Without seeds, seedling, plowing and transplanting in the successive regrowth seasons, perennial rice is capable of surviving for many consecutive years (Zhang et al., 2017) which reduced the large materials and labour input in annual field (Huang et al., 2018), and could economize approximately half of the input of annual rice and obtain more profit in rice production (Fig. 2). Moreover, with the absence of tillage, perennial rice cropping system reduced soil disturbance, would control soil erosion effectively and benefit for soil amelioration (Denardin et al., 2019). Perennial rice is an economic and environmental safely cropping system, and is able to produce a stable and sustainable grain yield over successive seasons across years.

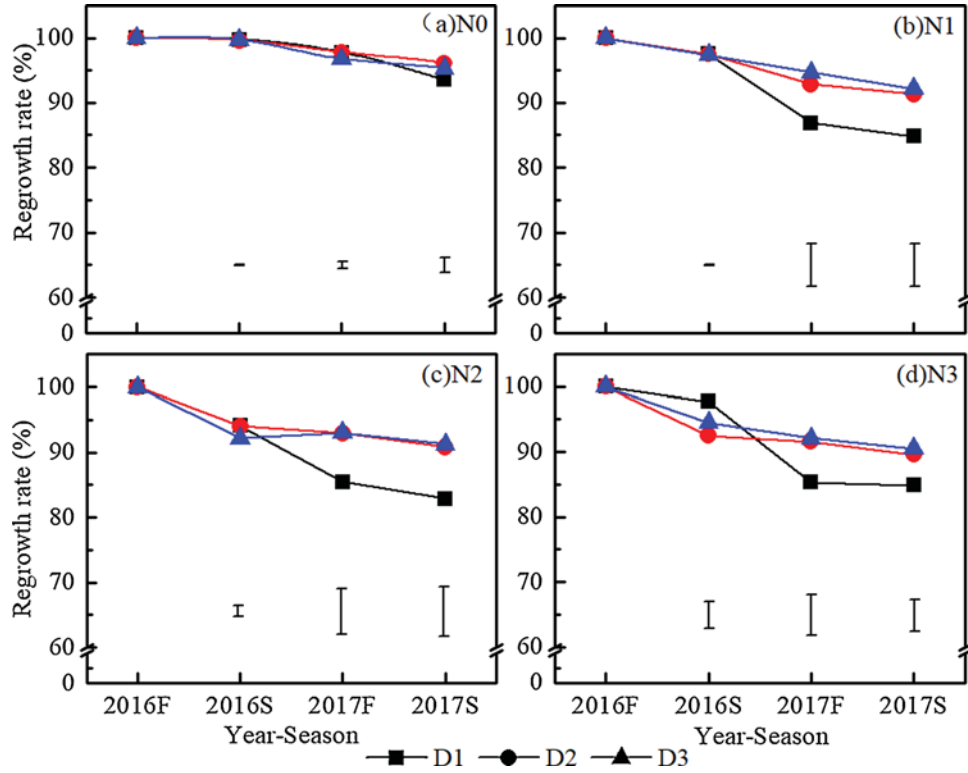


Fig. 5. Regrowth rate of perennial rice under different N rates and planting densities in 2016–2017. 2016F: first season in 2016 (transplanting season). 2016S: second season in 2016. 2017F: first season in 2017. 2017S: second season in 2017. Vertical bars represent the standard error for different treatments.

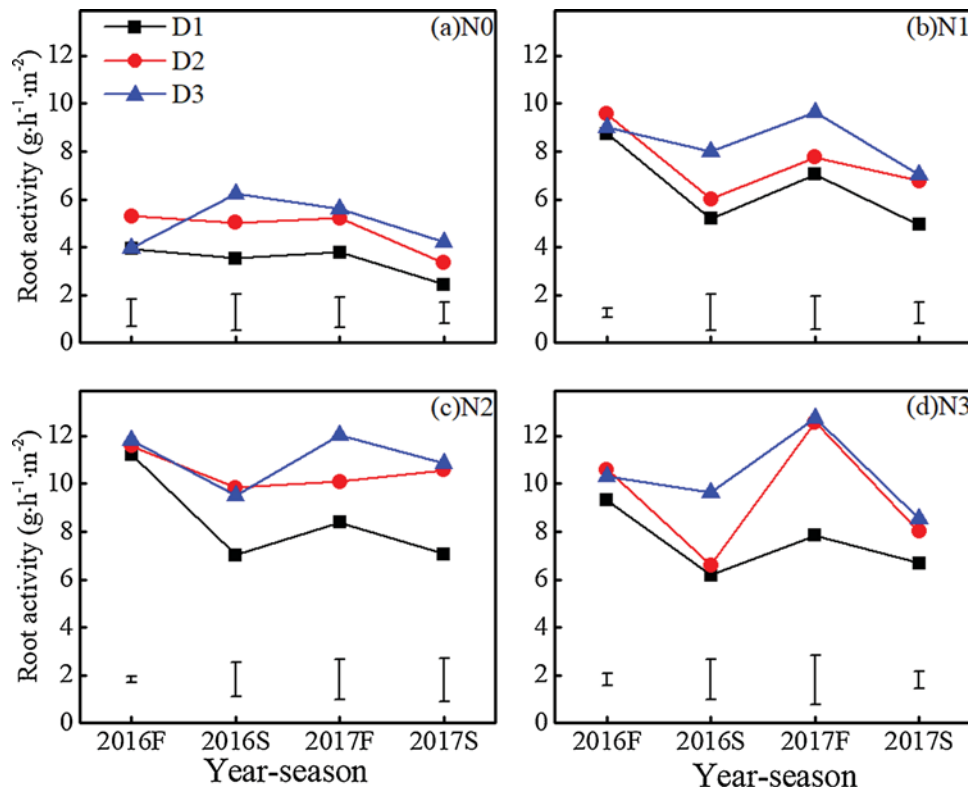


Fig. 6. Root activity of perennial rice under different N rates and planting densities in 2016–2017. 2016F: first season in 2016 (transplanting season). 2016S: second season in 2016. 2017F: first season in 2017. 2017S: second season in 2017. Vertical bars represent the standard error for different treatments.

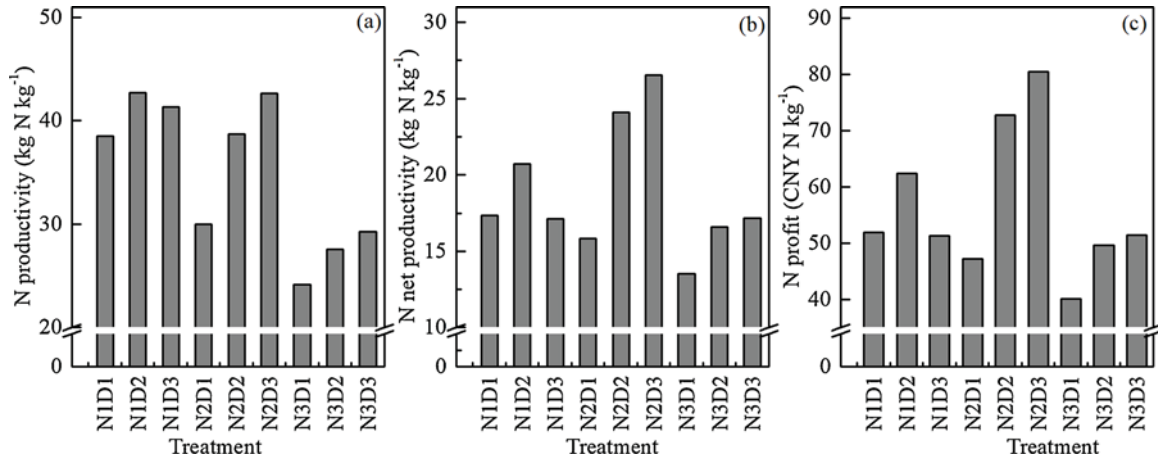


Fig. 7. The N productivity and profit of perennial rice. (a) The N productivity of each treatment. (b) The net productivity of each treatment. (c) The N profit of each treatment.

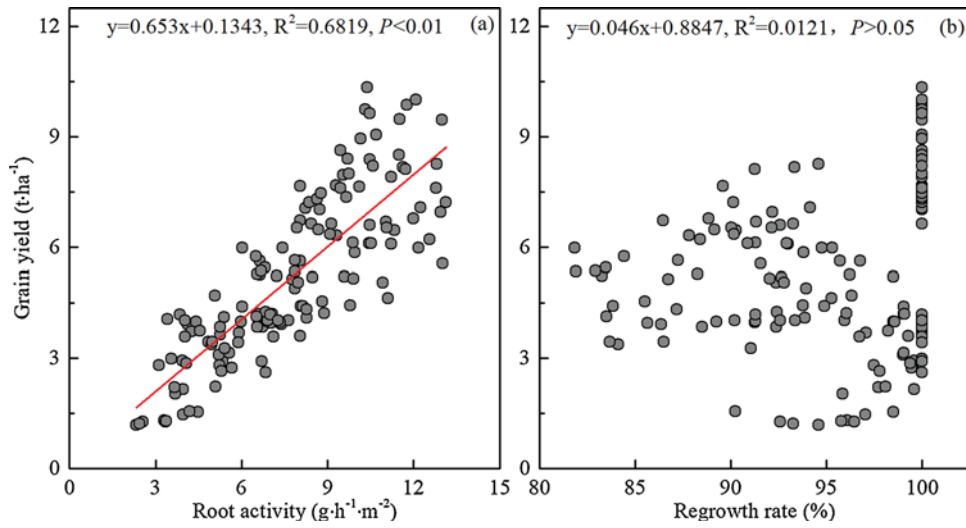


Fig. 8. The relationship of grain yield with root activity and regrowth rate of perennial rice. (a) The relationship of root activity with grain yield. (b) The relationship of regrowth rate with grain yield.

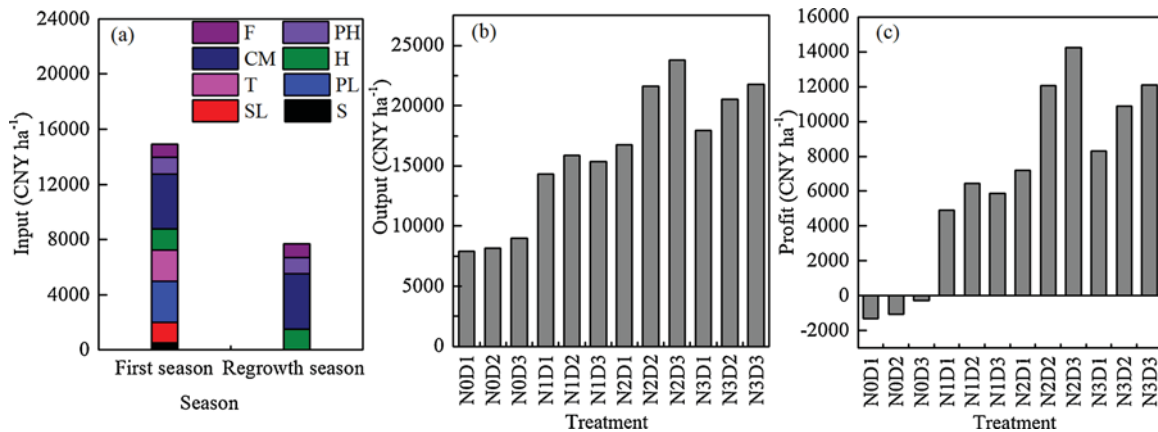


Fig. 9. The average input, output and profit of perennial rice in 2016-2017. (a) The input of transplanting and regrowth season. The total input including: F, fertilizer. PH, pesticide and herbicide. CM, crop management. H, harvest. T, transplanting. PL, plowing. SL, seedling. S, seeds. (b) The average output of each treatment. (c) The average profit of each treatment.

5.2. Regrowth rate and root activity

An optimal rice population and robust plants often have great potential to obtain high grain yield (Shen et al., 2013). For perennial rice, a high regrowth rate and root activity are critical for maintaining a robust rice population over successive regrowth seasons. In this experiment, the regrowth rate of perennial rice significantly decreased across seasons, but the grain yield remained stable. This pattern is likely benefit from the strong regrowth ability and self-regulation via new tillers from rhizome of perennial rice. Perennial rice had great regrowth ability that derived from the parent of *O. longistaminata* (Zhang et al., 2017, 2019c; Huang et al., 2018). Additionally, rice, including perennial rice, has a robust ability to self-regulate to maintain a healthy crop community (in terms of panicle no. m^{-2}) (Yang et al., 2014). Till the fourth season, the regrowth rate of perennial rice was still above on 90 %. Based on the high regrowth rate of perennial rice, the ability of perennial rice to self-regulate would compensate for the minor decrease that occurs in the rice population, which also likely explains why the regrowth rate showed a decreasing trend and why the panicle no. and grain yield of perennial rice remained at high and stable levels during the regrowth seasons (Tables 4 & 5).

The regrowth rate decreased as N rate increased, suggesting that N fertilizer limits the regrowth of perennial rice. This may be some physiological or genetic mechanism of perennial rice response to N fertilizer which is studying by our team now. Similar N effect was observed on sugarcane that high N fertilizer would limit the emergence rate and shooting rate in ratooned years (Zeng et al., 2020). As perennial rice is the first released perennial grain over the world in 2018, similar phenomenon on other perennial grains is not yet found now. However, as planting density increased, the regrowth rate of perennial rice increased, suggesting that controlling plant densities can contribute to sustainable regrowth. The result was consistent with the previous research on sugarcane that rational high planting density would lead to higher shooting rate and tillers in ratoon years (Qiu et al., 2019). These observations also explain why the N2D3 treatment produced the highest grain yield across years. Specifically, the positive effect of a high planting density in D3 on the regrowth and self-regulation ability of perennial rice compensated for the negative effect of N2 on regrowth. To sustainably produce perennial rice, chemical N fertilizer inputs need to be reduced within an appropriate range to ensure an adequate grain yield while high planting densities are maintained. Additionally, dense planting and less N fertilizer are the most effective and environmentally friendly ways for increasing yield and reducing N loss (Zhu et al., 2016).

Plants exchange substances and energy with the surrounding environment primarily via their roots (Yang et al., 2004; Zhang et al., 2019a). As a consequence, higher root activity reflects more water, nutrient and energy exchange with the environment (Liu et al., 2020; Zhang et al., 2019b) and results in a higher grain yield. Root activity was significantly related to the grain yield of perennial rice (Fig. 8a), high levels of root activity are essential to ensure a higher crop yield (Zhang et al., 2019b) and regrowth rate in the regrowth seasons. The root activity of perennial rice remained stable over successive regrowth seasons suggests that perennial rice had developed a root system that could absorb enough soil nutrients and water during the regrowth season (Pimentel et al., 2012), as the roots did not degenerate over successive regrowth seasons. The root activity of N2 was significantly higher than the other N rates, demonstrating that modest quantities of N fertilizer are capable of promoting the growth and activity of the root system. Indeed, low or excessive application of chemical N fertilizer limited the root growth and activity of rice (Zhang et al., 2019b). Moreover, the high planting density in D3 promoted higher root activity in the unit area in the field and then resulted in high root activity in N2D3. Thus, crop management that combines an appropriate N fertilizer rate and plant density coupled with the no-tillage can promote high root activity and support the sustainable production of perennial rice for several years.

5.3. Grain yield and its components

Perennial rice is a new cultivar of rice. Grain yield and yield components are the main metrics for assessing the success of the perennial rice 23 cultivar (Zhang et al., 2017, 2019c). In this experiment, the successful and stable grain yield of perennial rice over several seasons showed that this novel rice production system, which does not require tillage, can facilitate the sustainable production of perennial rice in an environmentally feasible manner (Huang et al., 2018). In this experiment, the N2D3 treatment produced the most stable and highest grain yield over four successive seasons across two years. This finding is likely attributed to the high root activity of tillers from rhizome and the greater ability of perennial rice to self-regulate documented in N2D3, which supports a robust rice population and an adequate supply of nutrients needed for perennial rice growth. Proper fertilizer and field management could help farmers obtain a high- and good-quality grain yield, reduce labour inputs and increase economic profits (Huang et al., 2018; Cui et al., 2018; Tilman et al., 2011). Based on the significantly positive correlation between root activity and panicle no. m^{-2} , spikelet no. panicle⁻¹ and grain weight, the high root activity in the N2D3 treatment enhanced the yield components and grain yield over successive regrowth seasons of perennial rice (Table 4).

The grain yield and yield components of N2 and N3 were not significantly different; however, these components were significantly higher for N2 and N3 than those for N0 and N1. This finding is illustrated by the fact that the N2 rate had a stronger positive effect on perennial rice production and the fact that the use of additional N fertilizer had no significant positive effect on the grain yield and yield components (Guo et al., 2010). In contrast, the use of more fertilizer in N3 resulted in a low seed-setting rate (Table 4). Excessive application of N fertilizer had no positive effect on the crop yield but instead resulted in a yield loss (Guo et al., 2010; Peng et al., 2006). Indeed, over-fertilization has been shown to reduce fertilizer use efficiency and increase fertilizer loss and pollution (Peng et al., 2006; Hossain et al., 2005). Planting density also had a significant effect on the grain yield. Both D2 and D3 had high yield potential, but D3 had higher regrowth potential and root activity (Table 5).

5.4. N productivity and economic benefits

Nitrogen (N) is an essential element of proteins, nucleic acids, enzymes, hormones and chlorophyll and plays an important role in maintaining the nutrient cycle and determining plant growth (Xu et al., 2020; Fowler et al., 2013). In this experiment, N fertilizer had a significantly positive relationship with panicle no. m^{-2} , spikelet no. panicle⁻¹, root activity and grain yield. These patterns illustrated that the addition of modest levels of N fertilizer can enhance both crop growth and crop yield (Ren et al., 2017). However, in recent years, increases in fertilizer loss and pollution have become more widespread as N fertilizer has often been excessively applied to increase crop yield, resulting in increased soil degeneration and environmental problems (Cai et al., 2020; Tian et al., 2016; Zhao et al., 2016; Zhang et al., 2018). In China, fertilizer use efficiency has been estimated to be 25 %, which is far below the worldwide average of 42 % (Chen et al., 2014). However, fertilization does not always increase crop yield; indeed, the excessive use of fertilizer can result in low fertilizer use efficiency, decrease economic profits and create environmental problems (Peng et al., 2006; Tian et al., 2016). N productivity was effective indicator for evaluating N fertilizer productivity (Wang et al., 2018). The N3 treatment in this experiment did not result in significantly higher grain yields compared with the N2 treatment; however, the N net productivity (Fig. 7) were significantly lower. Moreover, for perennial rice, high N fertilizer also limited its regrowth across successive seasons. Therefore, N fertilizer productivity needs to be improved to obtain a high crop yield.

Compared with annual rice, the absence of seeds, seedling, plowing and transplanting of perennial rice in regrowth seasons reduced the

intensive works in field and huge investment in materials that could obtain more profit in rice production (Huang et al., 2018). The fact that the highest values of N net productivity and N profit were observed in the N2D3 treatment demonstrated that the N fertilizer effect and productivity was the most optimal in this treatment, maximizing the grain yield, reducing fertilizer loss and pollution and enhancing regrowth.

6. Conclusion

- (1) Perennial rice is an economic and environmental cropping system, and was able to produce a stable and sustainable grain yield over successive seasons across years.
- (2) The N2D3 (180 kg ha⁻¹ nitrogen integrated with 22.7 plants m⁻²) treatment resulted in a high and stable grain yield with high root activity and regrowth rate of perennial rice for successive regrowth seasons across years, and resulted in more economic benefit and less N loss and pollution. Thus, the N2D3 treatment provided optimal conditions and economic profit for sustainable perennial rice production.
- (3) Generally, sustainable production of perennial rice at a certain grain yield requires a modest application of N chemical fertilizer coupled with a high planting density to maintain a high regrowth rate and reduce fertilizer loss.
- (4) The optimal conditions for the management of perennial rice have been poorly explored. Thus, our findings demonstrate the benefits of perennial rice production and suggest that the potential benefits of producing other perennial grains should be further examined.

CRediT authorship contribution statement

Yujiao Zhang: Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft. **Guangfu Huang:** Investigation, Data curation, Supervision. **Shilai Zhang:** Investigation, Supervision. **Jing Zhang:** Investigation, Supervision. **Shuxian Gan:** Investigation, Supervision. **Mao Cheng:** Investigation, Supervision. **Jian Hu:** Investigation, Supervision. **Liyu Huang:** Supervision. **Fengyi Hu:** Conceptualization, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors report no declarations of interest.

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Genotype by environment interactions for performance of perennial rice genotypes (*Oryza sativa* L./*Oryza longistaminata*) relative to annual rice genotypes over regrowth cycles and locations in southern China

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ABSTRACT

Genotype by environment (GxE) interactions for performance of 5 perennial rice genotypes (*Oryza sativa* L./*Oryza longistaminata*) were examined relative to 1 mutant and 3 annual rice genotypes over 2–6 growth cycles at 7 locations in southern China between 2014 and 2017. Environment main effects accounted for 25.7% of the total sum of squares (SS), with genotype 33.8% and GxE 37.7%. Cluster analysis identified 6 genotype × 6 environment groups, which accounted for 77.9% of the GxE-SS. Principal component axes 1, 2 and 3 accounted for 54.7%, 25.1% and 9.4% of the GxE-SS, respectively, with PCA1 indicating yield potential, PCA2 performance over ratoon cycles, and PCA3 ratoon percentage. Environment groups differed in yield potential, which related to site favourability and whether it was low or high in the ratoon cycle. Genotype groups differed in yield potential and how well they performed in higher ratoon cycles. The medium-maturity (125 days) seasonally-replanted annual rice check BN21 was highest yielding (6.13 t ha⁻¹). Perennial rice PR23 was high yielding and stable (5.25 t ha⁻¹), with earlier maturity (119 days) and strong regrowth (82%). Ratooned annual rice RD23 was high yielding in original crops but poor yielding in ratoon crops, with a low ratoon percentage (16.5%). Similarly, perennial Bt71 and ratooned BN21 were high yielding in original crops and low-cycle ratoons under favourable conditions, but yielded poorly in high-cycle ratoons and less favourable conditions, with moderate regrowth (59.6%). Despite strong regrowth (77.5%), perennials 264 and Bt69 had low yield, as did perennial 139A and mutant TZ, and both these groups were late maturity. A combination of high yield potential, strong regrowth and earlier maturity resulted in higher performance of perennial rice over environments and regrowth cycles, with PR23 outstanding, and able to perform similarly to the seasonally-replanted annual check, BN21, over up to six growth cycles. Ratoon performance and trade-offs need to be examined further.

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1. Introduction

With global population increasing, pressure on the resource base, and the impact of climate change, even marginal lands, which currently support 50% of world population and are at risk of degradation under annual cropping, must be farmed sustainably in future to meet the ever-increasing demands for food and livelihood (Eswanan et al., 1999; Tilman et al., 2011). Perennial grains show promise in meeting these conflicting needs for protection of fragile lands, while also allowing farmers to support themselves and their families (Glover et al., 2010). To do so, perennial grains must stabilize land and soil resources, while at the same time contributing grain and/or forage in mixed crop-livestock systems (Batello et al., 2014). In rice-based systems, with population rising rapidly, favourable land with access to irrigation largely utilized, and marginal lands of low fertility dependent on rainfall and vulnerable to climate change being increasingly asked to meet the food gap, the need to develop perennial rice as a component of sustainable intensification is urgent (Wade, 2014).

Following successful hybridization between *Oryza sativa* L. and *Oryza longistaminata* (Tao and Sripichitt, 2000), efforts to develop perennial rice commenced (Hu et al., 2003; Sacks et al., 2006; Zhang et al., 2014), with the long-term goal of breeding perennial rice to stabilize the fragile soils in rainfed lowland and rainfed upland rice-based farming systems. Three papers have specifically reported on performance of perennial rice in the field (Zhang et al., 2017; Huang et al., 2018; Samson et al., 2018), and as indicated below, perennial rice may have promise in a number of rice-based systems, and this requires further investigation.

Perennial rice derivatives were reported to survive, regrow and yield successfully across a diverse range of environments in southern China and Lao PDR, with perennial rice PR23 identified as a prime candidate for release to farmers, based on its broad adaptation and high yield over environments (Zhang et al., 2017). Other genotype groups showed preferential adaptation, to dry season, wet season, or more tropical conditions. The paper concluded that regrowth success and maintenance of spikelet fertility over regrowth cycles were important for adaptation of perennial rice, especially to low minimum temperature at higher altitude, and rainfall deficit in lower-altitude sub-humid conditions.

Huang et al. (2018) then examined the suitability of PR23 for release to farmers under irrigated paddy conditions, by comparing perennial rice PR23 with two seasonally-replanted annual rice genotypes, RD23 and HXR7, across 9 ecological regions in southern Yunnan Province of China, and across scales, from experimental plots to small-holder fields to commercial areas. Overall, the grain yield of PR23 was similar to those of the preferred annual rice cultivars in these conditions, but the economic analysis indicated substantial labour savings for farmers by growing the perennial instead of the annual. PR23 was considered acceptable in grain size and grain quality, so farmers were keen to grow PR23, because of reduced costs and especially labour savings.

Samson et al. (2018) extended these comparisons to rainfed lowland environments in the subhumid tropics of Lao PDR. While yields were lower in the ratoon crop, all perennial rice derivatives were able to survive the dry season with access to life-saving irrigation. This was promising, as the annual rice RD23 was unable to ratoon under these conditions, and had to be re-sown. Ratoon grain yields of several perennial rice lines were comparable to replanted annual RD23, which was also promising under those wet-season rainfall-deficit conditions.

This study aimed to extend this series by comparing selected perennial rice genotypes with annual rice genotypes allowed to ratoon, and with an annual rice genotype which was replanted each season as a control. A range of locations differing in altitude were used for comparisons across successive growth cycles. The objectives were 1) to examine G x E interactions among perennial rice, ratooned annual rice and replanted annual rice genotypes over locations and growth cycles,

2) to identify traits associated with improved performance, especially in higher ratoon cycles, and 3) to consider the implications and research questions.

2. Materials and methods

2.1. Planting location, experimental design and plot management

The experiments were conducted in 19 site-season-year (Environment E) combinations, at Jing Hong (21° 59' N, 100° 44' E), Puer (22° 45' N, 100° 51' E), Hong Ta (24° 24' N, 102° 32' E), Wen Shan (23° 23' N, 104° 13' E), Yuan Yang (23° 8' N, 102° 40' E), Lan Cang (22° 26' N, 99° 58' E) and De Hong (24° 26' N, 98° 35' E) in Yunnan Province of southern China. The sites at Jing Hong and Puer were continued for three years, with the remaining sites continued for two years only. There was potential for up to two crops per year to be harvested each year, from the wet and dry seasons, respectively. While rice may ratoon or reshoot from basal nodes after harvest in suitable conditions (Douthwaite et al., 1995), ratoon potential is expected to be stronger in perennial rice derivatives (Samson et al., 2018).

At each site, a randomised complete blocks design was used, comprising 9 genotypes with 3 replications. Long-term weather data showed minimum temperatures were lower at the higher altitude sites (Supplementary Table 1), so only one dry season crop could be harvested each year, except at Jing Hong. Annual rainfall ranged from 808 mm at Yuan Yang to 1587 mm at Lan Cang (Supplementary Table 2), with most rain falling between May and October at all sites. Consequently, data were available for G x E analysis from a total of 19 environments (Table 1), which for simplicity are referred to by their environment code, e.g. Jing Hong in the dry season of 2014 for the original crop in the ratoon cycle is referred to as J4D1, with subsequent ratoon crops there as J4W2, J5D3, J5W4, J6D5 and J6W6 (Table 1).

Soils at the experimental sites were generally fertile, with soil pH averaging 5.89, organic C 30.6 g kg⁻¹, total N 1.76 g kg⁻¹, available P 25.2 mg kg⁻¹, and exchangeable K 122.4 mg kg⁻¹ (Supplementary Table S3). Each site received 108.0, 31.9 and 87.1 kg ha⁻¹ of N, P and K respectively as a basal dressing. After puddling, each site was established by transplanting from adjacent seedbeds. Plot sizes of 3.30 m x 2.00 m were used, with a row spacing of 0.20 m, and with hills within the row spaced at 0.15 m apart. A further 72.0 kg N ha⁻¹ was applied at booting. After harvest, stubble was cut to 10 cm, so that consistent stubble for regrowth was available. Each site had access to irrigation, which was used to support growth during the dry season.

2.2. Germplasm and traits evaluated

Five perennial rice genotypes, obtained from the cross between *O. sativa* cv. RD23 and the wild species *O. longistaminata*, were chosen for this study (Table 2), including PR23, which had been reported to have high yield and broad adaptation over environments (Zhang et al., 2017). Other than PR23, four perennial lines thought to have promise or to differ in adaptation (Zhang et al., 2017) were also included, for comparison with PR23, mutant TZ, and three annual *O. sativa* treatments, for 9 genotype treatments in all (Table 2). BN21 was used as a seasonally-replanted annual rice check, as it is a locally-popular *indica* lowland rice cultivar grown widely by farmers in Yunnan province, due to its high grain yield and its exceptional grain quality, although at some sites, a local cultivar with reputedly similar characteristics and genetic background to BN21 was substituted for BN21, due to local preference (www.ricedata.cn/variety/varis; Table 2). In the second annual rice treatment, BN21 was not replanted, but allowed to ratoon, as annual rice is able to regrow to some extent (Douthwaite et al., 1995), and this provided a contrast with the putatively greater ratooning ability of the perennial rices (Samson et al., 2018). Likewise, RD23 was used as an additional ratooned annual check, because it is a parent of the five perennial rices and a popular *indica* lowland rice

Table 1
The 19 environments used to discriminate annual and perennial rice genotypes.

No	Site	Altitude (m)	Season	Year	Env Code	Sow or Re-sow ^a	TP ^b	CT ^c	FL ^d	Mature ^e	Duration ^f (d)	Regrowth ^g (%)	Yield ^h (t ha ⁻¹)
E1	Jing Hong	550	Dry	2014	J4D1 ⁱ	2014-1-17	2014-2-17	n.a.	2014-5-11	2014-6-18	121	n.a.	5.88
E2	Jing Hong	550	Wet	2014	J4W2	2014-7-11	2014-8-6	2014-8-4	2014-10-15	2014-11-21	109	84.1	1.34 ^j
E3	Jing Hong	550	Dry	2015	J5D3	2014-12-23	2015-1-25	2015-1-25	2015-5-16	2015-6-14	141	80.3	3.57
E4	Jing Hong	550	Wet	2015	J5W4	2015-6-23	2015-7-17	2015-7-15	2015-10-13	2015-11-9	118	72.3	3.15
E5	Jing Hong	550	Dry	2016	J6D5	2015-12-19	2016-1-30	2016-1-30	2016-5-4	2016-6-3	125	66.6	2.47
E6	Jing Hong	550	Wet	2016	J6W6	2016-7-2	2016-8-1	2016-8-1	2016-11-1	2016-12-1	123	45.2	2.07
E7	Puer	1305	Dry	2014	P4D1	2014-3-3	2014-4-16	n.a.	2014-7-18	2014-8-18	124	n.a.	5.28
E8	Puer	1305	Dry	2015	P5D2	2015-3-15	2015-5-11	2015-3-15	2015-6-15	2015-8-13	140	82.1	2.82
E9	Puer	1305	Dry	2016	P6D3	2016-3-16	2016-4-16	2016-3-18	2016-7-4	2016-8-13	141	71.9	1.9
E10	Hong Ta	1630	Dry	2014	H4D1	2014-3-6	2014-4-30	n.a.	2014-8-18	2014-9-14	137	n.a.	4.14
E11	Hong Ta	1630	Dry	2015	H5D2	2015-4-5	2015-5-5	2015-4-20	2015-7-8	2015-9-16	146	75.5	2.83
E12	Wen Shan	1260	Dry	2015	W5D1	2015-4-22	2015-6-2	n.a.	2015-8-23	2015-10-14	134	n.a.	5.88
E13	Wen Shan	1260	Dry	2016	W6D2	2016-4-15	2016-5-20	2016-5-14	2016-8-5	2016-9-17	125	51.3	2.27
E14	Yuan Yang	1034	Dry	2015	Y5D1	2015-2-28	2015-4-11	n.a.	2015-7-10	2015-8-12	124	n.a.	3.97
E15	Yuan Yang	1034	Dry	2016	Y6D2	2016-3-5	2016-4-10	2016-4-10	2016-7-11	2016-8-11	123	66.5	0.95
E16	Lan Cang	1150	Dry	2015	L5D1	2015-2-28	2015-4-25	n.a.	2015-7-10	2015-8-10	107	n.a.	3.66
E17	Lan Cang	1150	Dry	2016	L6D2	2016-3-5	2016-4-23	2016-3-21	2016-7-7	2016-8-9	137	70.4	1.86
E18	De Hong	900	Dry	2016	D6D1	2016-4-22	2016-5-22	n.a.	2016-8-7	2016-9-2	118	n.a.	4.53
E19	De Hong	900	Dry	2017	D7D2	2017-2-23	2017-3-27	2017-3-27	2017-7-10	2017-8-9	136	20.4	0.74
	Mean										130	66.4	3.10
	L.s.d. (P < 0.05)										1	6.2	0.35

^a The date of sowing in the original season, and the date of re-sowing of seasonally-replanted annual rice BN21 (G9) in subsequent ratoon seasons.
^b The date of transplanting in the original season, and the date of re-transplanting of seasonally-replanted annual BN21 (G9) in subsequent ratoon seasons.
^c The date of stubble cut-off to 10 cm after harvest, for the next ratoon season of G1-G8; but for seasonally-replanted BN21 (G9), this is not applicable (n.a.).
^d The average date of flowering in G1-G9 except those not booting.
^e The average date for maturity in G1-G9 except those not booting.
^f Days from transplanting to maturity in the original season, or days from stubble cut-back to maturity in the ratoon season.
^g The average regrowth percentage of G1-G8; but for the original season, and for seasonally-replanted BN21 (G9), this is not applicable (n.a.).
^h The average yield of G1-G9 except those not booting.
ⁱ The environment code in bold type is the first crop in the cycle at each site.
^j Very serious rice hopper and rat damage occurred in the wet season of 2014 at Jing Hong.

Table 2

Genotypes evaluated in perennial rice experiments in 19 environments in southern Yunnan, China. Perennial rice genotypes were derived from the cross between *Oryza sativa* cv. RD23 and *O. longistaminata*.

No	Genotype	Code	Growth Habit	Crop Type	Rice Type	Adaptation Response ^a	SW-TP (d)	TP-FL (d)	CT-FL (d)	FL-MT (d)	Height (cm)	Regrowth (%)	Yield (t ha ⁻¹)
G1	2011_HN_FS_0264	0264	Perennial	Interspecific	<i>Indica</i>	Dry Season	41	99	94	38	112	74.5	1.97
G2	2011_HN_Bt69	Bt69	Perennial	Interspecific	<i>Indica</i>	Dry Season	41	100	99	34	113	78.9	1.92
G3	2011_HN_Bt71	Bt71	Perennial	Interspecific	<i>Indica</i>	Dry Season	41	77	90	35	126	78.0	3.78
G4	2011_HN_139-12	139A	Perennial	Interspecific	<i>Indica</i>	Poor	41	101	92	34	111	79.4	0.78
G5	Mutant TZ	TZ	Perennial	Interspecific	<i>Japonica</i>	Wet Season	41	112	114	34	138	77.2	1.08
G6	PR23	PR23	Perennial	Interspecific	<i>Japonica</i>	Broad	41	74	91	34	98	81.2	5.25
G7	RD23	RD23	Annual	Improved cv	<i>Indica</i>	Broad	41	84	88	35	104	16.3	3.28
G8	BN21 ^b	BN21	Annual	Improved cv	<i>Indica</i>	Broad	41	83	89	39	102	37.4	3.73
G9	Replanted BN21 ^b	A-BN21	Annual	Improved cv	<i>Indica</i>	Broad	37	85	NA	41	104	NA	6.13
	Mean						41	91	94	36	112	66.4	3.10
	l.s.d. (P < 0.05)						1	1	1	1	3	4.7	0.27

^a Adaptation is either broad, season-specific or poor; based on data from Zhang et al. (2017); Samson et al. (2018) and Huang et al. (2018).

^b BN21 was replaced by similar genotypes in E7-E11 (CJ28), E12-13 (WD11), E14-E15 (HXR7), E16-E17 (DL201), and E18-E19 (DY8).

cultivar released in Thailand, which is widely grown across south-east Asia, because of its broad adaptation, photoperiod insensitivity, high yield potential, good disease resistance and high grain quality (Chakhonkaen et al., 2012). The mutant line TZ, an off-type from line TZ, had been observed to ratoon strongly in breeding nurseries over cycles, so was included for comparison as another ratooned annual rice line (Zhang et al., 2017). Genotypes are referred to by their genotype code, e.g. 2011_HN_FS_264 is line 0264 (Table 2).

Field duration (days) was calculated from dates of transplanting and maturation, and successive cycles of stubble cut-off and maturation. Grain yield (t ha⁻¹), plant height (cm), rice ratooning rate (percent of plants with regrowth), ratoon tiller number (tillers per plant), and effective panicle number (fertile panicles per plant) were recorded from 0.9 m sections of the central four rows of each plot (24 plants or 0.9 m²). Ten panicle samples were used for panicle length (spikelets per panicle), grain number per panicle (grains per panicle), seed set rate (grains per spikelet), and grain size (weight of 1000 grains in g). Grain number per square metre (m⁻²) was calculated from grain yield and grain size.

2.3. Statistical analysis

Yield data for 9 genotypes and 19 environments were extracted from appropriate single-site analyses of variance. Gx E interactions were analysed using the pattern analysis tool in CropStat 7.2 (IRRI, 2007). This method involved the joint application of cluster analysis and ordination to a transformed Gx E matrix. Since the objective was to understand genotypic adaptation for breeding, the Gx E matrix was transformed by environment standardisation (Cooper, 1999). The transformed data were clustered using an agglomerative hierarchical algorithm based on minimising incremental sum of squares (Ward, 1963). Scores for both genotypes and environments from the two-component interaction principal components model (IPCA) were computed for Axes 1, 2 and 3, and plotted as biplots, with environment points at the end of vectors labelled as in Table 1, and genotype points as symbols with labels as in Table 2. Patterns of grain yield were examined for genotype groups over environment groups, with means for all parameters compared using l.s.d. with appropriate degrees of freedom for main effects and interactions (Steel and Torrie, 1960).

3. Results

3.1. Environments

Long-term mean monthly minimum temperature was below 15 °C for 3 months at Jing Hong and Yuan Yang (Dec–Feb), 5 months at De Hong and Wen Shang (Nov–Mar), 6 months at Lan Cang (Nov–Apr), and

7 months at Puer and Hong Ta (Oct–Apr), which demonstrated a clear association between increasing altitude and prolonged low temperature during winter (Supplementary Table 1). In contrast, long-term mean monthly maximum temperature was generally mild at all sites, and only exceeded 28 °C for 1 month at Lan Cang (Mar), 5 months at Jing Hong (Feb–Jun), 6 months at De Hong (May–Oct), and 9 months at Yuan Yang (Mar–Nov), mostly at sites below about 1000 m (Supplementary Table 1). Long-term mean monthly pan evaporation exceeded 100 mm for 3 months (Mar–May) at De Hong, Lan Cang and Puer, and for 4 months at Jing Hong and Hong Ta (Mar–Jun). The exceptions were the most easterly site at Wen Shang (1260 m), where pan evaporation exceeded 100 mm for 4 months in the wet season (May–Aug), and at YuanYang, where temperatures were higher, and evaporation exceeded 100 mm in every month of the year (Supplementary Table 1).

Rainfall was higher in the west (Lan Cang, Puer and De Hong - 1500 mm) than in the east (Hong Ta, Yuan Yang and Wen Shang - 870 mm), with Jing Hong intermediate (1137 mm) (Supplementary Table S2). At all sites, monthly rainfall was lower in the dry season (Nov–Dec to Mar–Apr) than in the wet season. While there were dry spells in some years at individual sites relative to their long-term rainfall, irrigation was used so that water deficit was minimal. Soils at the experimental sites were mildly acidic and generally adequate in soil nutrients (Supplementary Table S3), though available P was marginal at Jing Hong (7.58 mg kg⁻¹). Nevertheless, the fertilizers applied at each site ensured nutrients were sufficient.

Site mean yield ranged from 0.74 t ha⁻¹ at De Hong in the 2017 dry season to 5.88 t ha⁻¹ at Jing Hong in the 2014 dry season and Wen Shan in the 2015 dry season (Table 1). Yields were generally lower in the wet season than in the dry season at Jing Hong, and in higher ratoon cycles at all sites. Genotype mean yield ranged from 0.78 t ha⁻¹ in perennial rice line 139A to 6.13 t ha⁻¹ in seasonally-replanted annual rice check BN21 (Table 2).

Environment main effects accounted for 25.7% of total sum of squares (T-SS), with genotype 33.8% and Gx E interactions accounting for 37.7% (Table 3). Stability regression accounted for only 24.1% of Gx E-SS. Cluster analysis on environment-standardised residuals identified 6 genotype groups x 6 environment groups, which preserved 77.9% of the Gx E-SS. The ordination analysis of these residuals indicated three interaction principal component axes, accounting for 54.7%, 25.1% and 9.4% of the Gx E-SS, respectively, or 89.2% in total (Table 3). The first two axes from ordination accounted for 79.8% of Gx E-SS, which preserved a similar proportion of the interaction variability to the 6 G x 6 E grouping identified by cluster analysis.

The dendrogram for environments from cluster analysis (Fig. 1a) initially separated higher-yielding (Fusion 35) from lower-yielding (Fusion 36) environments (Fig. 1a). Among higher-yielding environments, the original crops in cycle 1 (Fusion 3 – environment group E3,

Table 3

Cross site analyses of variance for G×E interaction studies on grain yield (t ha⁻¹) of 9 genotypes in 19 environments.

Source	dF	SS	MS	F	%TSS	%G×E-SS
Environment	18	1168.667	64.926	170.86**	25.65	
Genotype	8	1539.225	192.403	501.39**	33.78	
G × E	144	1717.739	11.929	31.39**	37.70	
Residual	342	131.240	0.384		2.88	
Total	512	4556.870				
Stability regression	8	413.9017	51.738			24.1
Regression Deviations	136	1303.8368	9.587			75.9
PCA component 1	25	939.603	37.584	15.19**		54.7
PCA component 2	23	431.152	18.746	7.58**		25.1
PCA component 3	21	161.467	7.689	3.11**		9.4
Residual	75	185.516	2.474			10.8
Total	144	1717.739				

and Fusion 31 – E31) separated from low-cycle ratoon crops at higher altitude (Fusion 29 – E29). Among lower-yielding environments, low-cycle ratoon crops at lower altitude (Fusion 32 – E32) separated from high-cycle ratoon crops at Jing Hong (Fusion 24 – E24) and wet-season ratoon crops at Jing Hong (Fusion 30 – E30).

For the biplots from ordination analysis (Fig. 2a and b), all environments were negative for Axis 1, while Axis 2 separated higher-yielding environments which were positive, from lower-yielding environments which were negative (Fig. 2a). Axis 3 separated low-cycle ratoon crops at lower altitude (E29) which were positive, from one original crop at Hong Ta 2014 (E3) and 2 wet-season ratoon crops at Jing Hong (E30), which were negative. Other original-crop environments (E31), low-cycle ratoon crops at higher altitude (E29) and high-cycle ratoon crops at Jing Hong (E24) were neutral for Axis 3 (Fig. 2b).

3.2. Genotypes and traits

In the dendrogram for genotypes from cluster analysis (Fig. 1b), a high-yielding group (Fusion 15) separated from the rest (Fusion 16), which in turn split into a moderate-yielding group (Fusion 13) and a low-yielding group (Fusion 14). Each of these yield groups then split

into two subgroups. The high-yielding group separated into perennial rice PR23 (Fusion 6 – G6) and seasonally-replanted annual rice BN21 (Fusion 9 – G9). In the moderate-yielding group, ratooned RD23 (Fusion 7 – G7) separated from the remainder (Fusion 11 – G11), which comprised perennial Bt71 (G3) and ratooned BN21 (G8). The low-yielding group split into Fusion 10 (G10) comprising perennial rice lines 264 (G1) and Bt69 (G2), and Fusion 12 (G12) comprising perennial rice line 139A (G4) and mutant TZ (G5).

In the biplots for genotypes from ordination analysis (Fig. 2a and b), Axis 1 separated the low-yielding genotype group which was positive, from the high-yielding genotype group which was negative, with the moderate-yielding genotype group intermediate (Fig. 2a). Axis 2 separated the moderate-yielding genotype group from the rest (Fig. 2a). Axis 3 strongly separated perennial rice PR23 (G6) which was negative, from seasonally-replanted BN21 (G9) which was positive (Fig. 2b).

Grain yields are presented for 6 G × 6 E groups from cluster and ordination analysis (Table 4a). Among environment groups on average, the original crops were highest yielding (E31 and E3), followed by lower-cycle ratoon crops from higher altitudes (E29), with the remainder low yielding (E32, E24 and E30). Among genotype groups on average, PR23 (G6) and replanted BN21 (G9) were high yielding; RD23 (G7), and Bt71 and ratooned BN21 (G11) were intermediate; and lines 264 and Bt69 (G10) and line 139A and mutant TZ (G12) were low yielding. PR23 was generally high yielding in all environment groups, and topped the ranking in E29 and E30. Replanted BN21 was often high yielding, topping the rankings in E29, E32 and E24, but was lowest yielding in the singleton group E3, the original crop at Hong Ta in the 2014 dry season. RD23 was highest yielding in original crops (E3, E31), but low yielding in all ratoon crops. Likewise, G10 (lines 264 and Bt69) were high yielding in E3, but otherwise performed poorly. G11 (Bt71 and ratooned-BN21) was lowest yielding in the high-cycle ratoon and wet-season ratoon crops in Jing Hong (E24 and E30). G12 (line 139A and mutant TZ) did poorly everywhere, but especially in E31, E29 and E32.

For field duration (Table 4b), perennial rice PR23 (G6) was early maturity (119 days) and relatively stable, with field duration only varying by 30 days over environment groups. The early-mid duration groups G9 (replanted BN21) and G11 (Bt71 and ratooned BN21) were also stable, with their field durations varying by 26–31 days. In

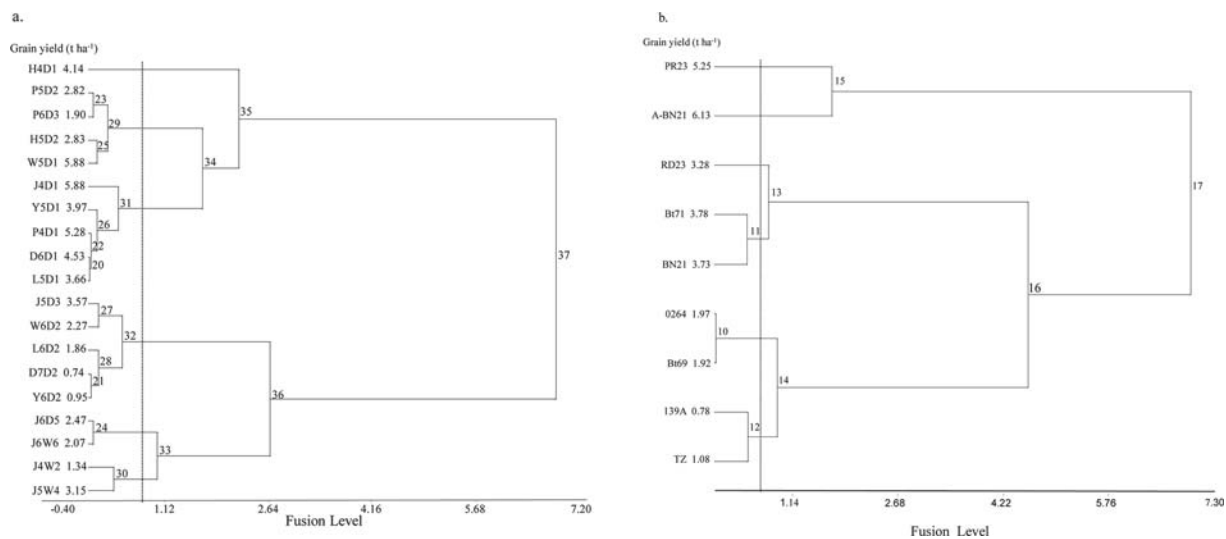


Fig. 1. a. Environment groupings applied to standardised yield data for nine perennial rice genotypes (*Oryza sativa* L., cv. RD23/*Oryza longistaminata*). The dendrogram shows fusion levels at which the groups join. The fusion level is proportional to the increase in within group SS at each fusion. The vertical dashed line represents the truncation of 19 environments into six groups using Ward's agglomerative clustering algorithm. Refer to Table 1 for environment abbreviations. b. Genotype groupings applied to standardised yield data for nine perennial rice genotypes (*Oryza sativa* L., cv. RD23/*Oryza longistaminata*) over 19 environments. The dendrogram shows fusion levels at which the groups join. The fusion level is proportional to the increase in within group SS at each fusion. The vertical dashed line represents the truncation of nine genotypes into six groups using Ward's agglomerative clustering algorithm. Refer to Table 2 for genotype abbreviations.

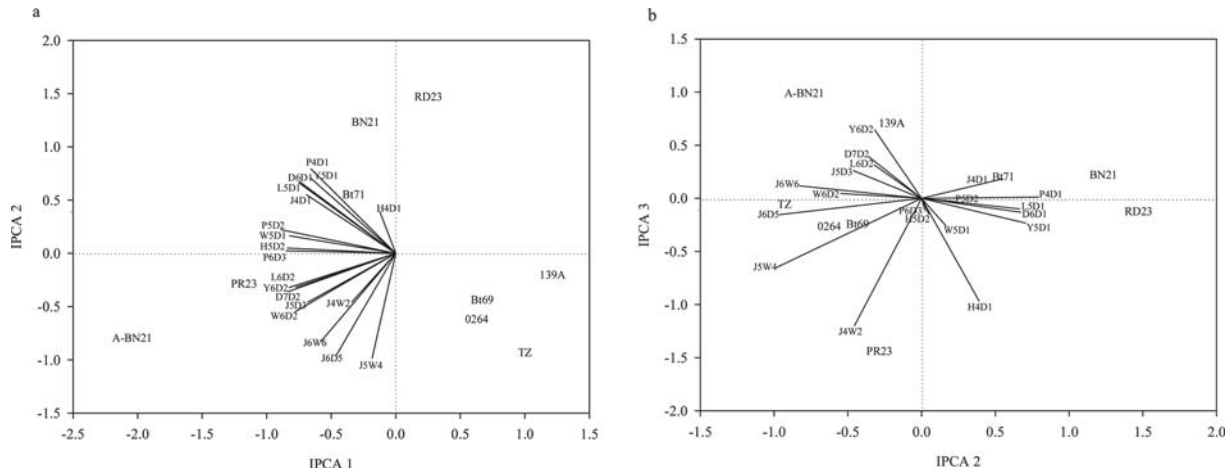


Fig. 2. Principal component analysis (environment standardised) of the environment x genotype interaction for (a) Axis 1 and Axis 2, and (b) Axis 2 and Axis 3, for grain yield over 19 environments and nine perennial rice genotypes (*Oryza sativa* L., cv. RD23/*Oryza longistaminata*). Refer to Tables 1 and 2 for genotype and environment abbreviations. The Gx E interactions for Axis 1 and Axis 2, and for Axis 2 and Axis 3, accounted for 79.8% and 34.5% of the sum of squares, respectively ($P < 0.01$).

Table 4

a) Grain yield ($t\ ha^{-1}$), b) growth duration (d), and c) rice ratoon percentage (%), of 6 genotype groups across 6 environment groups (l.s.d. = 0.99 for grain yield, 1 for growth duration, and 17.5 for rice ratoon percentage, respectively; $P < 0.05$).

Genotype Group	E3 (1)	E31 (5)	Environment E29 (4)	Group E32 (5)	E24 (2)	E30 (2)	Mean
Yield ($t\ ha^{-1}$)							
G6 (1)	7.30	6.94	7.24	2.88	2.59	3.63	5.25
G7 (1)	8.25	8.19	1.82	0.49	0.25	1.48	3.28
G9 (1)	1.65	7.54	7.33	6.34	5.66	2.36	6.13
G10 (2)	6.43	1.77	1.03	1.61	2.27	2.46	1.94
G11 (2)	3.60	6.94	5.06	1.51	0.80	1.58	3.75
G12 (2)	0.00	0.65	0.81	0.48	2.31	2.18	0.94
Mean	4.14	4.60	3.35	1.88	2.14	2.21	3.10
Duration (d)							
G6 (1)	124	107	137	117	125	112	119
G7 (1)	136	117	131	149	110	108	128
G9 (1)	117	116	130	140	118	114	125
G10 (2)	169	132	135	145	126	113	135
G11 (2)	123	112	140	128	116	109	123
G12 (2)	M ^a	135	163	145	135	121	142
Mean	137	122	142	138	123	113	130
Ratoon (%)							
G6 (1)	n.a. ^b	n.a.	91.7	77.9	65.1	89.4	82.0
G7 (1)	n.a.	n.a.	5.6	11.1	12.1	56.4	16.5
G9 (1)	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
G10 (2)	n.a.	n.a.	86.4	64.7	78.9	90.0	77.5
G11 (2)	n.a.	n.a.	82.3	44.9	41.4	68.9	59.6
G12 (2)	n.a.	n.a.	88.6	77.0	64.7	79.6	79.1
Mean	n.a.	n.a.	76.5	57.8	55.9	77.9	66.4

Numbers of group members in parentheses.

^a M = no booting.

^b n.a. = not applicable, as ratoon percent can only be recorded from regrowth.

contrast, the medium duration (128 days) RD23 (G7) and late (142days) lines 139A and mutant TZ (G12) were more variable in field duration, varying by 41–42 days. Lines 254 and Bt69 (G10) were late maturing (135 days) and most variable in field duration, with a range of 56 days. Field duration was greater (140 days) in low-cycle ratoon crops (E29 and E32), compared to original crops in E31 and E3 (130 days) and high-cycle ratoon crops (118 days). Ratoon percentage was consistent over environment groups, with poor regrowth in RD23 (16.5%), moderate regrowth in Bt71 and BN21 (G11), and strong regrowth in PR23 (G6), lines 264 and Bt69 (G10), and lines 139A and TZ (G12).

3.3. Trait associations

The main effects of environment group and genotype group on trait expression are shown in Table 5. The 5 high-yielding original crops in E31 had field duration of 122 days, were 115 cm in height, had 6 panicles per plant, 130 grains per panicle with 0.59 grains per spikelet, 18500 grains m^{-2} , 1000 grain weight of 23.4 g, and a grain yield of 4.60 $t\ ha^{-1}$. Relative to E31, the singleton original crop at Hong Ta 2014 (E3) was delayed in maturity by 15 days, was 21 cm shorter in plant height, had 2 fewer panicles per plant, and grain yield was 0.46 $t\ ha^{-1}$ lower. The low-cycle ratoon crops at high altitude (E29) were 20 days later, had 25% fewer grains m^{-2} and 25% less yield than E31. Likewise, the low-cycle ratoon crops at low altitude (E32) were

Table 5
Main effect of environment and genotype groupings on yield components of annual and perennial rice genotypes.

	Growth duration (d)	Plant height (cm)	Ratoon percent (%)	Panicle length (cm)	Panicles per plant (pl ⁻¹)	Grains per Panicle (panicle ⁻¹)	Grains per spikelet (%)	Grain weight (g 1000 ⁻¹)	Grains per m ² (10 ³ m ⁻²)	Grain yield (t ha ⁻¹)
Environment	Group									
E3 (1)	137	94	NA	23.1	4.08	144	64.0	23.5	17.7	4.14
E31 (5)	122	115	NA	23.4	6.03	131	59.0	23.4	18.5	4.60
E29 (4)	142	112	76.5	21.0	6.25	115	77.0	24.3	13.8	3.35
E32 (5)	138	111	57.8	23.0	7.80	106	60.0	24.2	7.8	1.88
E24 (2)	123	105	55.9	22.3	7.48	107	83.0	21.5	10.6	2.14
E30 (2)	113	105	77.9	23.3	6.85	109	70.0	24.1	9.3	2.21
Mean	130	112	66.4	22.8	6.74	116	66.4	23.3	12.9	3.10
<i>L.s.d.</i> (<i>P</i> < 0.05)	1	4	6.2	0.9	1.10	12	3.7	0.9	1.4	0.35
Genotype	Group									
G6 (1)	119	98	82.0	19.1	10.49	105	76.0	24.5	21.4	5.25
G7 (1)	128	104	16.5	23.6	9.19	122	74.0	28.2	11.6	3.28
G9 (1)	125	104	NA	23.3	7.49	128	73.0	27.0	22.7	6.13
G10 (2)	135	112	77.5	24.1	5.57	121	65.0	19.2	10.1	1.94
G11 (2)	123	116	59.6	23.5	8.17	116	67.0	24.3	15.4	3.75
G12 (2)	142	122	79.1	22.7	3.32	106	53.0	21.5	4.4	0.94
Mean	130	112	66.4	22.8	6.74	116	66.4	23.3	12.9	3.10
<i>L.s.d.</i> (<i>P</i> < 0.05)	1	3	4.7	0.7	0.83	9	2.8	0.7	1.0	0.27

delayed 16 days in field duration, their regrowth was 57.8%, and their grains m⁻² and grain yield were both about 60% less than E31. In contrast, field duration was similar to E31 in the high-cycle ratoon crops at E24, but their plant height was 10 cm lower, their regrowth was 55.9%, grain size was down 10%, and their grains m⁻² and grain yield were down 45%. Conversely, the wet season ratoon crops (E30) were 9 days shorter in field duration, 10 cm less in plant height, showed strong regrowth, but both grains m⁻² and grain yield were halved relative to E31.

For genotype groups (Table 5), replanted BN21 (G9) was medium in maturity (125 days), short in plant height (104 cm), had 7.5 panicles per plant, 128 grains per panicle with 0.73 grains per spikelet, 1000 grain weight of 27.0 g, 22700 grains m⁻² and a grain yield of 6.13 t ha⁻¹. Relative to replanted BN21 (G9), perennial rice PR23 (G6) was 6 days earlier in field duration, 6 cm shorter in plant height, with strong regrowth (82%), 3 more panicles per plant, and similar grains m⁻² and grain yield overall. Perennial line Bt71 and ratooned BN21 (G11) had similar field duration to replanted BN21 (G9), were 12 cm taller, had 59.6% regrowth, but were about 40% lower in grains m⁻² and grain yield. Ratooned RD23 (G7) was also medium maturity and short in plant height, but its regrowth was poor (16.5%), so its grains m⁻² and grain yield were halved relative to G9. Lines 264 and Bt69 (G10) were 10 days longer in field duration and 8 cm taller with strong regrowth (77.5%), but all yield components were lower, so their grain yield was only 30% of G9. Finally, lines 139A and mutant TZ (G12) were 17 days longer in field duration, 18 cm taller with strong regrowth (79.1%), with the lowest values for all yield components, for 85% yield reduction on G9.

These trait associations can be summarised using Pearson correlation analysis (Supplementary Table 4). Among environments, grain yield was positively correlated with grains m⁻² and grains panicle⁻¹ (*P* < 0.05), but negatively with panicles m⁻² (*P* < 0.10). Among genotypes, grain yield was positively correlated with grains m⁻² (*P* < 0.05), grains spikelet⁻¹ (*P* < 0.05) and panicles m⁻² (*P* < 0.10), but negatively with field duration (*P* < 0.05) and plant height (*P* < 0.10). Other internal correlations followed, such as field duration being positively correlated with plant height (*P* < 0.10).

4. Discussion

In this study, G×E interaction accounted for 37.7% of the total sum of squares for grain yield, which, together with Genotype, accounted for 71.5% of the total variation. Three vectors accounted for 89.2% of

G × E, suggesting a high repeatable component, which was consistent with other studies in annual rice (Botwright Acuna et al., 2008) and perennial rice (Huang et al., 2018). The genotype groupings of lines 139A and TZ (G12) and of lines 264 and Bt69 (G10) were consistent with the previous study of Zhang et al. (2017), which indicated a strong component of repeatable interaction, which was also consistent with other studies (Wade et al., 1999). Consequently, cluster and ordination analysis reduced the matrix from 9 genotype treatments × 19 environments (=171) to 6 genotype groups × 6 environment groups (= 36), whilst retaining the repeatable variation for interpretation.

4.1. Environment groupings

In contrast to earlier studies in perennial rice (Zhang et al., 2017; Samson et al., 2018), the majority of the environments here were conducted with irrigation in the dry season, and the three wet season environments at Jing Hong had adequate rainfall (Supplementary Table 2), so rainfall and temperature (Supplementary Table 1) had only a secondary impact on yield here. Consequently, the 19 environments were grouped by cluster and ordination analysis into distinct environment groups that could be defined by their yield potential, and by which crop in the ratoon cycle they represented, as explained below.

The highest yields (4.60 t ha⁻¹) were attained by the five original crops at Jing Hong, Yuan Yang, Puer, De Hong and Lan Cang (E31), and trait expression in this environment group can be taken as the standard for comparison under favourable conditions, using the principles explained by Sengxua et al. (2017). Hong Ta 2014 (E3) separated, as replanted BN21 failed there, perhaps due to pre-flowering stress, since field duration was extended and plant height and panicles plant⁻¹ were reduced in E3 relative to the favourable standard E31. The third group with high yields (3.35 t ha⁻¹) comprised four environments from early ratoon cycles in the higher-altitude locations at Puer, Hong Ta and Wen Shan (E29), where conditions were mild and favourable for regrowth (Supplementary Tables 1 and 2). In contrast, the three low-yielding groups (E32, E24, E30) averaged only 2.01 t ha⁻¹, half that of the high-yielding groups. E32 comprised 5 environments from early ratoon cycles in less favourable environments at Jing Hong, De Hong, Yuan Yang, Lan Cang and Wen Shan (1.88 t ha⁻¹), which generally were lower in altitude with higher temperatures than those in E29, so weather had a secondary role in the environment groupings. Both of the remaining low-yielding environment groups comprised ratoon crops from Jing Hong only, the lowest altitude site, which could support two crops per year, and which ran for three years. E30 comprised wet season crops in

cycles 2 and 4, with a mean yield of 2.21 t ha⁻¹, while E24 comprised high-cycle ratoon crops (cycles 5 and 6) with a mean yield of 2.14 t ha⁻¹. Thus environments grouped strongly by whether they were original crops, low- or high-cycle ratoons, with their expression modified by seasonal favourability, and if wet or dry season.

4.2. Genotypes and traits

The nine genotypes were grouped by cluster and ordination analysis by their responses to the environment groups above. This is clearly illustrated in the biplots (Fig. 2), where Axis 1 represented yield potential, separating the high-yielding groups G9 (Replanted-BN21) and G6 (PR23) to the left, from intermediate-yielding groups G7 (RD23) and G11 (Bt71 and BN21) to the middle, and low-yielding groups G10 (Lines 264 and Bt69) and G12 (Lines 139 A and TZ) to the right (Fig. 2a). Axis 2 related to ratoon performance, which separated the intermediate-yielding RD23 (G7) and Lines Bt71 and BN21 (G11), which performed well in original crops but poorly in ratoon crops, due to their lower ratoon percentages. Axis 3 separated the high-yielding perennial rice PR23 (G6) from the Replanted BN21 (G9), with other genotype groups intermediate (Fig. 2b). This can be interpreted as ratoon success, with low yield in ratoon neutral, and high yield positive or negative on Axis 3, depending upon whether high performance was due to replanting (BN21 – G9) or ratooning (PR23 – G6).

Table 4 summarised these relationships clearly, and was fully consistent with the biplots (Figs.2a, b). Replanted BN21 (G9) did well everywhere, except at Jing Hong 2014 Dry Season, when early stress presumably was a disadvantage to its establishment of a high yield potential. There was a clear advantage for PR23 (G6) in being high in yield potential, earlier in field duration, and strong in regrowth. Other perennial and ratooned annual rice groups performed less well, depending upon how they were able to regrow in subsequent cycles, and in addition, their later maturity was also a disadvantage. Other yield components were consistent with these relationships (Table 5), as confirmed by the Pearson correlations (Supplementary Table 4). PR23 (G6) demonstrated desirable phenotypic characteristics, such as good grain size, with other reports suggesting PR23 also had favourable grain quality, milling and taste characteristics (Huang et al., 2018).

4.3. Implications

The superiority of PR23 for release to farmers as a high-yield, stable, widely-adaptable perennial-rice cultivar is again demonstrated in this paper, consistent with our earlier reports (Zhang et al., 2017; Huang et al., 2018; Samson et al., 2018). Further, this paper now establishes the capability of PR23, and perennial rice, to successfully regrow and yield for up to six cycles in the field (from one planting for two regrowth cycles per year over three years). Huang et al. (2018) have also shown the economic advantage of growing the perennial rice over the annual rice, because of reduced requirements for labour as a result of not having to transplant, and hence, increased profitability with reduced drudgery for the farmer's family. Other perennial rice lines tested were also able to regrow successfully in the field, whereas annual rices, especially RD23, were very poor in regrowth capacity, which was consistent with Samson et al. (2018).

In relation to regrowth, it was notable that the second crop at Jing Hong in 2014, in the wet season, was severely damaged by rice hoppers and rats, and yielded only 1.34 t ha⁻¹ on average (Table 1). Despite this severe damage, the perennial rices survived, and yields recovered to over 3.00 t ha⁻¹ in both ratoon crops in 2015, and over 2.00 t ha⁻¹ in both ratoon crops in 2016, especially in PR23 (G6) (Table 4a). This attests to a viable level of resilience among the perennial rice lines if adverse conditions are encountered, such as has been reported for low temperature (Zhang et al., 2017) or water deficit (Samson et al., 2018).

When this experiment was originally established in 2014, data from a number of our previous experiments with perennial rice had been

collected, but at that time, had not yet been properly analysed nor published. Entries were selected for this experiment based on the best evidence available at that time. Now that the previous work has been published (Zhang et al., 2017; Huang et al., 2018; Samson et al., 2018), we can reflect on our earlier choices. We chose three entries from what was to become genotype group G3 in Zhang et al. (2017): lines 264, Bt69 and Bt71 (Table 2). If the experiment were to be set up now, we would only select one perennial rice line from Zhang et al. in G3, perhaps line 264, and replace Bt69 and Bt71 with line 246 (from Zhang et al. in G4) and line 56 (from Zhang et al. in G6). This would ensure all of the adaptation groups identified by Zhang et al. (2017) were represented in this experiment. Nevertheless, changing the entries in this way would have been unlikely to have altered our conclusions, since PR23 was so dominant in its performance over environments, as it was in that previous report, and now, also in its performance over up to six seasons.

Promising new lines are now coming through the perennial rice breeding program, such as PR24, PR25 and PR101, and it will be interesting to see how they perform across environments, as they have been selected for alternative ecological niches. Recently, there have also been efforts to further broaden the scope of the breeding program, by back-crossing promising perennial rice lines with established cultivars adapted to different rice ecosystems and regions, such as upland and rainfed lowland rice cultivars from Asia, Africa and Latin America. Further crosses between *Oryza sativa* and *Oryza longistaminata* would also be warranted, to further broaden the genetic base available for selection. This would be especially so if F1 progeny of such crosses were inter-crossed, in order to develop and select segregating populations of perennial rice, whilst retaining consistent genetic composition, as advocated recently by Larkin et al. (2014) for perennial wheat. Such breeding approaches are expected to continue to provide promising lines of perennial rice for further evaluation.

Finally, the research reported here also draws attention to the need for further understanding of longevity in perennial rice. How many ratoon cycles can be grown before replanting is needed? Is there any systemic yield decline over ratoon cycles, and if so, can any such decline be arrested through improved management or improved disease resistance? What trade-offs may occur as a result of the perennial growth habit, and can they be compensated by any improved resource capture in the perennial? Are there benefits from including perennials, such as improved sustainability, biodiversity, soil health or livestock integration? Some of these challenges may be best addressed using long-term experiments, to ensure valid comparisons with error control, as is currently planned in China.

5. Conclusions

The results showed that perennial rice PR23 was widely adapted, and its yield was stable and comparable to the seasonally-replanted annual rice BN21, over diverse environments, and for up to six growth cycles (Table 4). Traits responsible for the adaptation of PR23 over environments and regrowth cycles included a high yield potential, earlier maturity and strong regrowth capacity (Table 4). The results also demonstrated the ability of PR23 and other perennial rice genotypes to recover from stresses in an earlier regrowth cycle, and increase subsequent grain yields, attesting to the resilience of these perennial rice genotypes (Table 4).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.fcr.2019.107556>.

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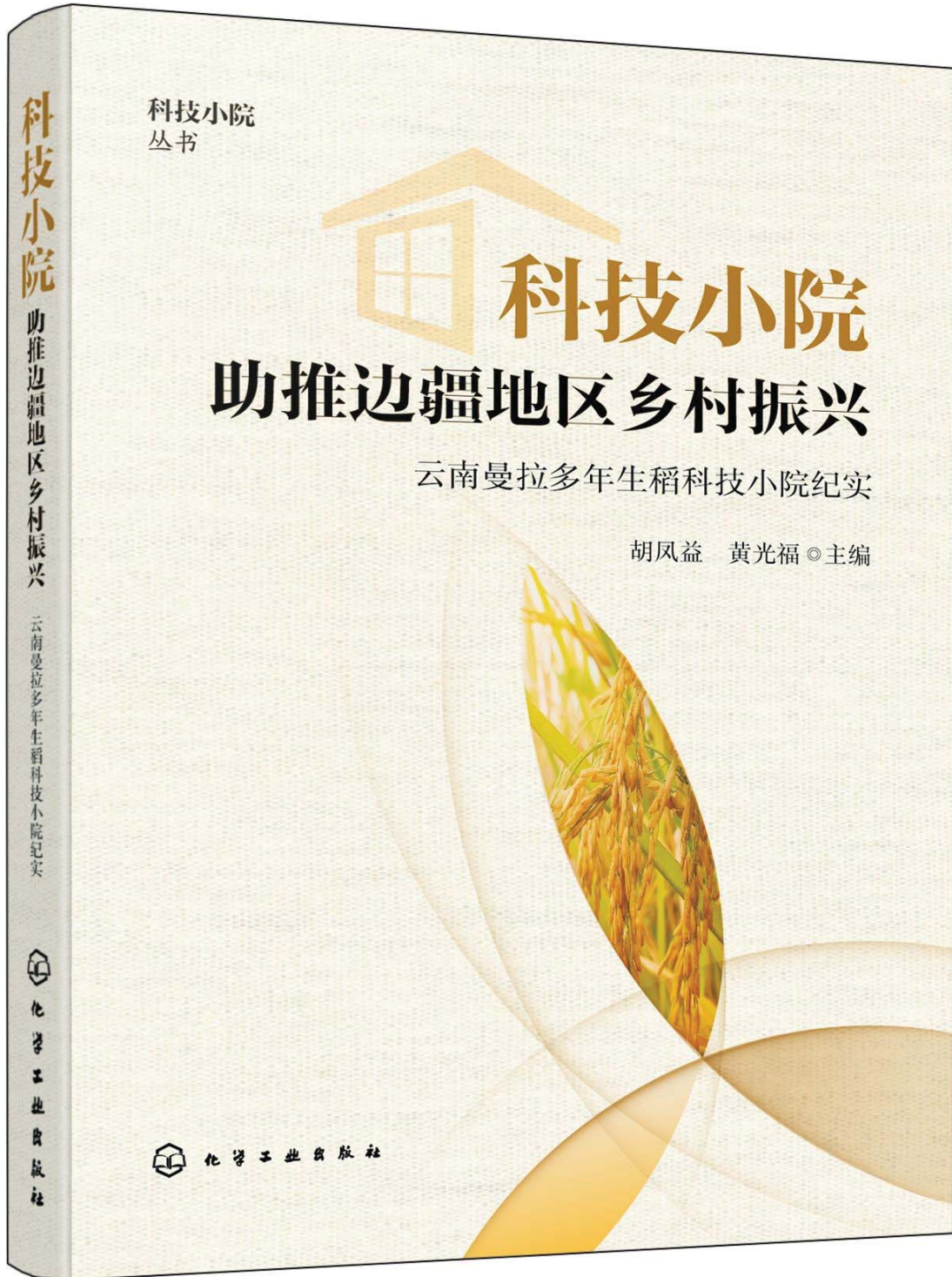
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内容提要

本书由长期驻扎科技小院的33位硕士研究生和博士研究生共同编写完成，记录了他们在科技小院期间开展的科技创新与社会服务的内心历程变化与感悟，他们用行动证明了自己的价值，也向农户、企业、政府部门展现了新时代农科研究生的风采。本书适合有志于深入基层实践的在校青年大学生了解“三农”，也适用于高等教育从业者和研究者了解新形势下的农业院校人才培养新模式。

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《科技小院助推边疆地区乡村振兴——
云南曼拉多年生稻科技小院纪实》
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前 言

云南大学胡凤益团队提出的利用长雄野生稻（*Oryza longistaminata*）地下茎（Rhizome）无性繁殖特性培育多年生稻（Perennial Rice, PR）设想。经过二十多年不竭地探索实践，培育出了具有生产应用价值的多年生稻23（PR23）、云大25（PR25）与云大107（PR107）等多个多年生稻品种，在全球多年生作物育种领域具有里程碑意义，实现了稻谷生产方式从一年生到多年生的转变。多年生稻技术是一项轻简化的稻作生产技术，多年生稻的秧苗是从上一年（季）稻桩地下茎的芽上生长出来，自第二年（季）起，基于越冬和免耕技术，稻谷生产不再需要买种、育秧、犁田耙田、栽秧等生产环节，实现了节本增效、降低劳动强度、减少劳动力投入与减轻农田水土流失等多维效益协调发展。

新农科如何培养人才？在全国农业专业学位研究生教育指导委员会的指导和帮助下，我们在云南省西双版纳州勐海县勐遮镇曼恩村委会曼拉村建立了多年生稻科技小院。小院有试验田100余亩，常年有5-10名研究生和2-3名年青老师驻扎。我们以小院为载体，把农业科技研发和农科人才培养进行结合，以培养农科学子的三农情怀，全面实地参与乡村振兴，实现学生德智体劳全面发展，真正做到农科学子成为祖国乡村振兴建设的主力军。



本书由长期驻扎科技小院的33位硕士研究生和博士研究生共同编写完成，记录了他们在科技小院期间开展的科技创新与社会服务的内心历程变化与感悟，他们用行动证明了自己的价值，也向农户、企业、政府部门展现了新时代农科研究生的风采。本书适合有志于深入基层实践的在校青年大学生了解“三农”，也适用于高等教育从业者和研究者了解新形势下的农业院校人才培养新模式。



目 录

- 001 我与科技小院的故事
- 005 我怀念的稻田岁月
- 012 微甜的回忆
- 015 不下农田不知“稻”
- 020 我与多年生稻的故事
- 025 初入曼拉，初识多年生水稻
- 028 迎着阳光，哗啵作响
- 034 科技小院——我的，我们的
- 038 江山客思满，云水稻田空
- 044 在多年生稻科技小院的日子，累并快乐着
- 048 做一个有情怀的科研人
- 054 勤耕读“慧”种稻——在田野中成长
- 060 从北方到南方插秧
- 065 傣园稻香——我的“上山下乡”之路
- 072 稻花香里说丰年
- 077 逐梦路上，与稻同行
- 082 我与我的科技小院

彩虹总在风雨后	086
与多年生稻的“缘”	090
在生命正芬芳的日子里，有稻作伴	095
科技小院：一场属于学农人的旅程	100
扎根农耕基层，谱写多年生稻新篇章	106
风吹稻香	111
承载着美好回忆的科技小院	115
苦与乐的科研生活	119
田里的金色晚霞	124
满满稻路忆	128
我与“多年生稻”的相识、相遇	134
乡村振兴，科技小院在路上	139
遇“稻”、知“稻”	142
不负青春，浓“农”情谊	145
喜看稻菽千层浪，遍地英雄下夕烟	150
金黄稻田，在驻守中看见传承的光	152



作为一名农业基层工作者，我们的任务是将我们所学的知识全部反馈于民，反哺于民，从群众中来到群众中去。我也会谨记胡凤益老师的教导和多年生稻科技小院的使命在三农工作中不断地努力下去，为边疆的三农发展贡献自己微薄的力量。

——李小波

多年生稻科技小院地理位置

多年生稻科技小院位于云南省西双版纳傣族自治州勐海县曼拉村民小组。勐海县东接景洪市，东北接思茅市，西北与澜沧县毗邻，西和南与缅甸接壤，自古有“滇南粮仓”之称，四季适宜水稻生长，盛产优质稻米，是国家级粮食生产基地，有着得天独厚的栽培条件。勐海县属热带、亚热带西南季风气候，冬无严寒、夏无酷暑，年温差小，日温差大。自然条件高温多雨，地形平坦开阔，年平均气温18.7℃，年均日照2088小时，年均降雨量1341毫米，境内河网密布，水资源丰富，全年有霜期32天左右。水稻主要分布于海拔600~1500米之间的坝区，共有47.7万亩。

多年生稻科技小院技术支持

多年生稻科技小院座落在在云南省西双版纳傣族自治州勐海县勐遮镇曼拉村云南大学田间试验站，长期有10名研究生及2-3名指导老师驻扎，拥有100余亩多年生稻品种选育、栽培技术研究试验基地。多年生稻科技小院是以云南大学胡凤益研究员带领的云南省多年生稻技术创新团队为核心，建有云南省多年生稻工程技术研究中心、云南省多年生作物国际联合研究中心、多年生稻技术示范推广云南省引智基地、种康院士工作站、钱前院士工作站等研究平台。该团队长期从事水稻多年生性基础理论研究、多年生稻品种培育、配套耕作栽培技术研究等工作。同时团队属于国际多年生作物协作组的成员，具有扎实的理论基础和国际领先的多年生稻研究成果。团队目前已和多家知名国外科研机构及院所建立了实质性合作，包括联合国粮农组织（FAO）、国际水稻研究所（IRRI）、缅甸曼德勒大学、泰国乌汶国家水稻研发中心、老挝国家农林科学院、越南北部山地农林科学院、柬埔寨棉芷大学、美国山地研究所、非洲稻作中心、乌干达国家农科院粮作中心等，为多年生稻科技小院的运作和发展提供了坚实的技术支撑。

Article

Density-Dependent Fertilization of Nitrogen for Optimal Yield of Perennial Rice

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Abstract: In the absence of tillage, perennial rice is an innovation and supplement to rice production. Proper N fertilizer application connected to planting density has been proposed as an effective way to improve rice yields. The tradeoff between crop N uptake and N supply is essential for optimal N management and soil environment benefit in the perennial rice cropping system. To assess the response of perennial rice to N fertilizer and planting density, field experiments with four consecutive growing seasons within two years, from 2016 to 2017, were conducted in southern China. Four nitrogen rates (N0, N1, N2, and N3 refer to 0, 120, 180, and 240 kg N ha⁻¹, respectively) combined with three planting densities (D1, D2, and D3 refer to 100 × 10³, 167 × 10³ and 226 × 10³ plants ha⁻¹, respectively) were designed. The results showed that both N rate and planting density significantly affected crop production ($p < 0.05$), N uptake and soil N balance. Specifically, the N2D3 mode could achieve sustainable and higher dry matter accumulation (15.15 t ha⁻¹) and grain yield (7.67 t ha⁻¹) among all the treatments over the four seasons. A positive relationship between N uptake and dry matter/grain yield was observed. The N2D3 mode showed significantly higher N uptake (201 kg ha⁻¹ each season) and less soil N loss (27.1%), relative to C.K. Additionally, the N2D3 mode could reach the optimal N balance (−0.2 kg ha⁻¹) with a low N requirement (23.9 kg N Mg⁻¹ grain), resulting in higher N use efficiency (NAE: 26.5 kg N kg⁻¹, NRE: 64.9%). In the perennial rice cropping system, therefore, 180 kg N ha⁻¹ integrated with 226 × 10³ plants ha⁻¹ could deliver higher grain yields with less N requirement, higher N use efficiency and less soil N loss. This optimal combination between planting density and nitrogen rate can result in soil N balance for sustainable perennial rice production.

Keywords: N balance; N fertilizer; N uptake; perennial rice cropping system; soil N loss



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1. Introduction

Due to the ongoing growth of the world population, the demand for food is under great pressure [1,2]. Rice is the staple food for more than half of the world's population, which faces more pressure than any other grain [3]. In rice production, chemical fertilizer addition, increasing the planting density and improving cultivated area are proposed to increase yields [4–6]. Due to the restricted arable land [7], fertilizer addition and increasing planting density are proposed as the main ways to improve the yield [8]. In particular, fertilizer has been proposed as the primary method for the strong desire of farmers to pursue high grain yields [9]. Overfertilization has been a common phenomenon for farmers. However, excessive or inappropriate fertilization does not always contribute to a high grain yield, which may result in low fertilizer use efficiency and cause a series of environmental problems [10–12]. The overall rice production mainly relies on annual rice with a plowing cropping system, which is an intensive work for farmers that needs

seeds, seedling, plowing, transplanting, crop management and harvest etc. annually, especially in terraces and mountains [13]. Annually plowing in the long term also intensifies soil erosion and degradation, which is not conducive to sustainable soil production and the environment [14].

Perennial rice is bred by the clone characteristics of the rhizome of *Oryza longistaminata* and could survive and produce for several successive seasons or years [13,15]. With the release of perennial rice cultivar 23 (PR23) in 2018, the revolution of rice production caused by perennial crops has started. From the second season or year, perennial rice could ratoon from the rhizome of the stubble of last season and produce for successive years [13,15–17]. Without tillage, seeding and transplanting, perennial rice reduced labor and material input, resulting in considerable economic profit for farmers [13,15]. The absence of tillage always reduces soil erosion and enhances soil properties, would achieve sustainable and environmental rice production and balance ecological and food security [15,18].

Nitrogen (N) is the essential element for perennial rice production. Increasing N fertilizer rate and planting density have been regarded as the most effective ways to improve the rice yield significantly [8,19]. However, unreasonable N management would result in low crop yields, along with severe environmental problems [20]. Generally, the averaged N application was 225 kg N ha⁻¹ and N fertilizer utilization efficiency was 35% in croplands of China [21], which often caused serious N loss and pollution. The optimal N fertilizer of perennial rice is often highly dependent on the planting density and soil productivity. Due to the short term of perennial rice release, the response of perennial rice to nitrogen and planting density in the perennial cropping system is still unclear. Based on grain yield increase, evaluating the response of perennial rice to N rate and planting density, soil N balance and loss, and N requirement could help us formulate optimal N management and access the soil environment in the perennial rice cropping system. Formulation of optimized N and planting density management would provide scientific guidance for farmers to plant rice environmentally. Thus, a field experiment with four N rates integrated with three planting densities was conducted to assess the dry matter accumulation and grain yield, plant nitrogen uptake and requirement, soil nitrogen balance and loss of perennial rice. The objective of this paper was to explore the response of perennial rice to N fertilizer and planting density, evaluate the productivity and soil nitrogen balance and loss in a perennial rice field, and formulate and provide proper N fertilizer management in a no tillage-perennial rice cropping system.

2. Materials and Methods

2.1. Site Description

This study was performed over four successive seasons from 2016 to 2017 at the Perennial Rice Research Station of Yunnan University, located in Gasa town (20°57′22″ N, 100°45′43″ E, altitude 555 m), Jinghong, southwestern China—a typically double rice area, which is characterized by a tropical monsoon climate. The average sum of rainfall recorded in the years 2016 and 2017 was 927.7 mm and 1342.6 mm (Figure 1), respectively, and most rainfall occurred from June to October. The average monthly temperature was 23.8 °C (Figure 1).

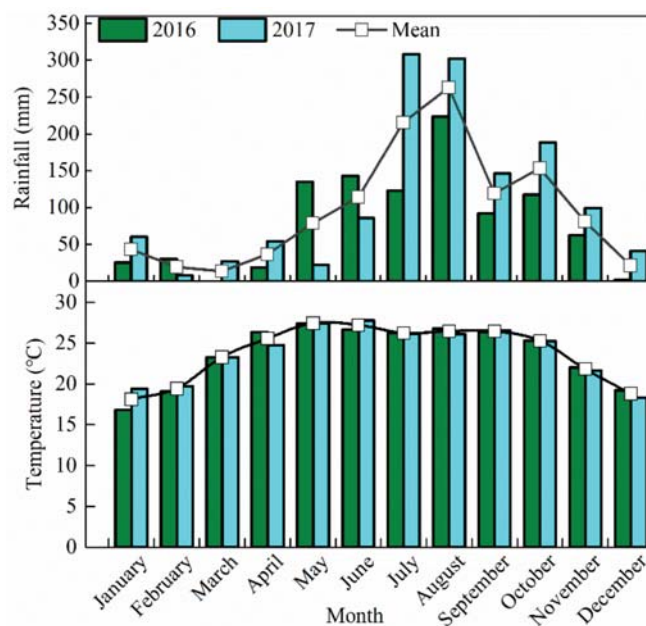


Figure 1. Rainfall and temperature in experimental site Jinghong from 2016 to 2017.

Before 2016, the prevailing rice system—annual rice with plowing annually—was conducted in the trial field. The soil was classified as a ferritic soil with 5.05 pH, 34 g kg⁻¹ soil organic matter, 2.1 g kg⁻¹ soil total nitrogen, 156 mg kg⁻¹ available soil nitrogen, 7.6 mg kg⁻¹ available soil phosphorus and 139 mg kg⁻¹ available soil potassium.

2.2. Experimental Design

A split-plot experiment with three replicates was applied over four successive seasons from 2016 to 2017, as 2016F (first season) and regrowth seasons 2016S, 2017F and 2017S. Four N rates, N0, N1, N2 and N3, with 0, 120, 180, and 240 kg N ha⁻¹ applied respectively were used as the main plots. Three planting densities included D1, D2 and D3 with 100 × 10³, 167 × 10³ and 226 × 10³ plants ha⁻¹, respectively, were used as subplots (Figure 2a). These four N rates and three planting densities generated the following twelve combinations: N0D1, N0D2, N0D3, N1D1, N1D2, N1D3, N2D1, N2D2, N2D3, N3D1, N3D2 and N3D3 (Figure 2a), each of them with an area of 20 m² size.

The cultivar perennial rice 23 (PR23) was selected as the material that was sowed on 15 Dec 2015 and transplanted in a plowing and level field on 30 January 2016, and harvested in late June and October each year (Figure 2c). After the harvest of each season, the rice stubble was cut back 5–10 cm above the ground to maintain the uniformity of new tillers arising from rhizomes and to depress tillers from the stem. The new tillers that emerged from the rhizome of the rice stubble were only maintained for successive regrowth seasons (2016S, 2017F and 2017S). Meanwhile, no-tilling was conducted across the successive regrowth seasons. During winter, perennial rice lies dormant in the soil and emerges when warmer temperatures return in the next year.

N fertilizer (urea) was manually and evenly spread at four stages 50% at the transplanting time for 2016F or new tillers emerging for regrowth seasons (2016S, 2017F and 2017S), 20% at the tilling stage, 20% at the heading stage and 10% at the filling stage, respectively. For all treatments, the fertilizer P and K were 90 kg ha⁻¹ and 180 kg ha⁻¹, respectively. The P fertilizer was once applied as the base fertilizer each season. The K fertilizer was used as a rate of 4:4:2 at the transplanting or cutting stubble, heading stage and 20 days after heading (to keep the root activity and promote the new tillers of perennial rice. For different planting densities, the plant spacing for D1, D2 and D3 were 27, 20 and 17 cm, respectively, and row spacings for these were 37, 30 and 26 cm, respectively.

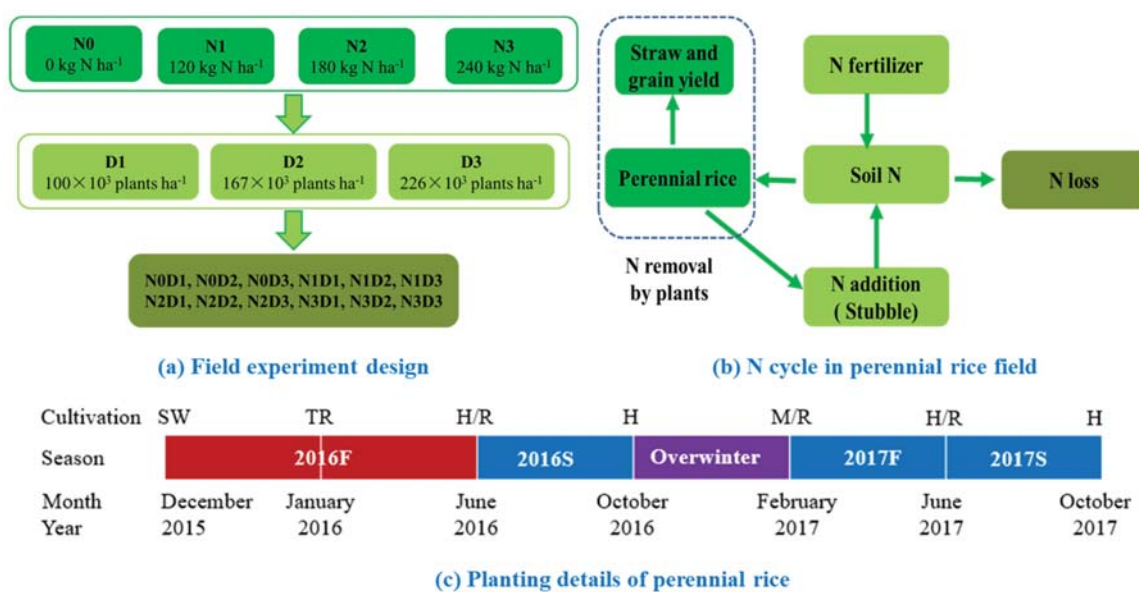


Figure 2. Field experiment design, planting details, and N cycle in the perennial rice field. (a) Field experiment design of different N rates and planting density. (b) N cycle in the perennial rice cropping system. (c) Planting details of perennial rice. SW, sowing. TR, transplanting. H, harvest. R, regrowth. M, stubble management (cutting back). 2016F, first season (red color) from sowing to the first harvest. 2016S, 2017F, and 2017S, three regrowth seasons (blue color) from regrowth to harvest each season. Overwinter, from the last harvest in the first year in winter to the first regrowth in the second year.

2.2.1. Irrigation Regime

The field was irrigated intermittently, and the details are as follows.

In the transplanting season of 2016, 3 cm water above ground was kept for 2 days and then plowed. Perennial rice was transplanted 2 days after plowing, and the field was kept in 3 cm water for 10 days. For the regrowth seasons of 2016 and 2017, the field should be kept 3 cm in water for 10 days after cutting rice stubble. When the rice leaf turns green in the transplanting season or the stubble regrowth is 1–2 tillers, the field should be kept in 1–2 cm water until the tillering stage to promote the tillering of perennial rice. When the tillers reached 75% of the objective total tillers, the field would be naturally dried to control the tillers. When the jointing stage is reached, 2–3 cm water should be kept until the heading stage of perennial rice. Fifteen days after heading, the rainy month arrives and the rice does not need more irrigated water for growth, meaning we naturally dried the field until harvest. In the winter, the field needs certain moisture to keep perennial rice alive and overwinter.

2.2.2. Field Management

Weeds Control

In general, we sprayed herbicide 5–7 days after transplanting in the first season or after tiller emergence in the regrowth seasons. Prometryn was applied to soil to control the gramineous weeds, broadleaf weeds and *Cyperaceae* weeds. Cyhalofop-butyl or fluroxypyr was used to control perennial weeds.

Pest Control

The main pests in this area are rice planthopper and *Cnaphalocrocis*. Thiamethoxam and pymetrozine were used to control the rice planthopper. Dursban and indoxacarb were used to control *Cnaphalocrocis*. The usage of pesticides was according to the emergence and condition of pests each year.

Disease Control

Perennial rice has high resistance to rice blast. This is derived from the parent of *Oryza longistaminata*, which has high resistance to rice blast and a strong rhizome. Therefore, the main disease in perennial rice field are *Xanthomonas oryzae*, *Rizicocotinia solani* and *Ustilaginoidea virens*. We controlled these three diseases at the tillering stage, metaphase differentiation of the young panicle or the start of heading. Azoxystrobin and tricyclazole were used to control *Xanthomonas oryzae*, chloroisobromine cyanuric acid and thiediazole copper were used to control *Rizicocotinia solani*, validamycin and isoprothiolane were used to control *Ustilaginoidea virens*.

2.3. Sampling and Analytical Methods

2.3.1. Grain Yield

At harvest time, grain yield and dry matter were manually harvested at an area greater than 5 m², and grain yield was weighted and adjusted to a 14% water content.

2.3.2. Soil and Plant Nitrogen

Soil nitrogen (N) and plant N were determined by using the Kjeldahl method [22]. Soil samples were taken at five points as “S” at 0–20 cm soil and dried naturally without sunshine, then milled by a grinding mill and sieved through a 0.25 mm screen for soil nitrogen analysis. The plant samples were collected and divided into grain, stem, leaf in three sections at harvest time, fixed at 105 °C and dried at 75 °C by using an air dry oven, then milled by a grinding mill and crushed and sieved through a 0.25 mm screen for plant nitrogen analysis. Plant N uptake, soil N loss, N balance, N requirement and N physical effect were calculated by the formulae as follows [23–25]:

$$N \text{ uptake (kg ha}^{-1}\text{)} = N\% \text{ in grain} \times Y_g + N\% \text{ in stem} \times Y_s + N\% \text{ in leaf} \times Y_l \quad (1)$$

$$N \text{ input (kg ha}^{-1}\text{)} = N \text{ application} + N \text{ addition by stubble} \quad (2)$$

$$N \text{ balance (kg ha}^{-1}\text{)} = \sum N_{\text{input}} - N_{\text{uptake}} \quad (3)$$

$$N \text{ loss (kg ha}^{-1}\text{)} = \text{soil based N variation (sowing-harvest)} + N \text{ input} - N \text{ uptake} \quad (4)$$

$$N \text{ requirement (kg Mg}^{-1} \text{ grain)} = \text{plant N uptake} / Y_g \quad (5)$$

$$N \text{ agronomic efficiency (NAE) (kg N kg}^{-1}\text{)} = \text{grain yield (Ni-N0)} / N \text{ application} \quad (6)$$

$$N \text{ recovery efficiency (NRE) (kg N kg}^{-1}\text{)} = \text{plant N uptake (Ni-N0)} / N \text{ application} \quad (7)$$

where Y_g is the grain yield, Y_s is the stem yield, Y_l is the leaf yield, $i \geq 1$.

2.4. Statistical Analysis

Split-plot analysis with three-way ANOVA (N rate and planting density were set as two fixed factors, and the season was set as a random factor) was used to assess differences of the significance of the main plot and subplot and interactions of the treatments. Before ANOVA, tests on normality (by a Shapiro–Wilks test of the residuals) and homoscedasticity (by a Bartlett test) were conducted. In cases when homogeneity of variances was not given by the original data, we classified the data, recombined the data in SPSSAU, and then the data met the requirements of ANOVA. Three replications were calculated for each measurement, and one-way ANOVA was used to compare the effects of the different treatments on the measured variables [15]. F-tests were conducted, and multiple comparisons were performed using the least significant difference test (L.S.D.) ($p \leq 0.05$). We analyzed the experimental data with the IBM SPSS statistical package v.20.0 (SPSS, Inc., Chicago, IL, USA), and the figures were generated using Origin 2015 (Sys Software, Inc., Northampton, MA, USA, 2015).

3. Results

3.1. Yield

3.1.1. Grain Yield

There was a significant difference in the grain yield of different treatments ($p < 0.05$) (Table 1). Season ($p < 0.001$), nitrogen ($p < 0.001$), density ($p < 0.05$) and the interaction effects of nitrogen with density ($p < 0.05$) and season, nitrogen and density ($p < 0.01$) all decided the grain yield of perennial rice. For the effects of N fertilizer, the N1, N2 and N3 significantly increased the grain yield by 82.2%, 148% and 141% compared with N0 (2.69 t ha^{-1}) ($p < 0.05$). For the planting densities, the D2 (5.34 t ha^{-1}) and D3 (5.64 t ha^{-1}) showed significantly higher grain yields than the D1 (4.59 t ha^{-1}) ($p < 0.05$). In the four seasons, N2D3 resulted in a significantly higher average grain yield, which was 7.67 t ha^{-1} .

Table 1. Dry matter accumulation of perennial rice under different N rates and planting densities over four seasons of 2016–2017.

Treatment	Leaf (t ha^{-1})	Stem (t ha^{-1})	Panicle (t ha^{-1})	Dry Matter (t ha^{-1})	Grain (t ha^{-1})
Season					
2016F	$1.08 \pm 0.43 \text{ b}$	$3.96 \pm 1.18 \text{ b}$	$7.50 \pm 2.39 \text{ a}$	$12.54 \pm 3.96 \text{ a}$	$7.26 \pm 2.15 \text{ a}$
2016S	$1.13 \pm 0.33 \text{ b}$	$4.65 \pm 1.76 \text{ a}$	$4.71 \pm 1.84 \text{ c}$	$10.49 \pm 2.76 \text{ b}$	$4.42 \pm 1.27 \text{ b}$
2017F	$1.50 \pm 0.13 \text{ a}$	$4.00 \pm 1.64 \text{ b}$	$5.17 \pm 1.43 \text{ bc}$	$10.68 \pm 2.54 \text{ b}$	$4.76 \pm 1.74 \text{ b}$
2017S	$1.36 \pm 0.47 \text{ a}$	$3.28 \pm 1.04 \text{ c}$	$5.79 \pm 1.89 \text{ b}$	$10.43 \pm 2.75 \text{ b}$	$4.32 \pm 2.05 \text{ b}$
N rates					
N0	$0.91 \pm 0.23 \text{ c}$	$2.55 \pm 1.01 \text{ d}$	$3.75 \pm 1.00 \text{ c}$	$7.22 \pm 2.45 \text{ c}$	$2.69 \pm 0.97 \text{ d}$
N1	$1.16 \pm 0.33 \text{ b}$	$3.88 \pm 1.56 \text{ c}$	$5.56 \pm 1.46 \text{ b}$	$10.59 \pm 2.77 \text{ b}$	$4.90 \pm 1.66 \text{ c}$
N2	$1.47 \pm 0.46 \text{ a}$	$4.59 \pm 2.11 \text{ b}$	$7.07 \pm 1.92 \text{ a}$	$13.14 \pm 4.37 \text{ a}$	$6.68 \pm 1.76 \text{ a}$
N3	$1.54 \pm 0.47 \text{ a}$	$4.87 \pm 1.79 \text{ a}$	$6.78 \pm 2.14 \text{ a}$	$13.19 \pm 4.09 \text{ a}$	$6.48 \pm 1.48 \text{ b}$
Planting density					
D1	$1.16 \pm 0.41 \text{ c}$	$3.40 \pm 1.69 \text{ c}$	$4.94 \pm 2.03 \text{ c}$	$9.49 \pm 4.15 \text{ c}$	$4.59 \pm 1.82 \text{ c}$
D2	$1.26 \pm 0.43 \text{ b}$	$3.96 \pm 1.72 \text{ b}$	$5.80 \pm 2.01 \text{ b}$	$11.02 \pm 4.03 \text{ b}$	$5.34 \pm 2.24 \text{ b}$
D3	$1.40 \pm 0.45 \text{ a}$	$4.56 \pm 1.79 \text{ a}$	$6.63 \pm 2.08 \text{ a}$	$12.59 \pm 4.15 \text{ a}$	$5.64 \pm 2.36 \text{ a}$
ANOVA					
S (df = 3)	7.330 **	9.120 **	5.792 *	2.729 (ns)	15.599 ***
N (df = 3)	17.185 ***	54.708 ***	11.529 **	28.399 ***	36.502 ***
D (df = 2)	12.319 **	22.538 **	10.116 *	25.797 ***	9.332 *
N × S (df = 9)	4.303 **	4.041 **	5.639 ***	9.051 ***	9.047 ***
D × S (df = 6)	1.391 (ns)	4.129 **	2.701 *	4.018 *	4.071 **
N × D (df = 6)	1.524 (ns)	2.979 *	2.554 (ns)	5.088 **	7.399 ***
N × D × S (df = 18)	1.757 *	1.040 (ns)	2.967 ***	1.916 *	2.521 **

Different letters within a column represent significant differences at $p < 0.05$ (LSD). S: season. N: nitrogen rate. D: planting density. N × S: interaction effect between nitrogen rate and season. D × S: interaction effect between planting density and season. N × D: interaction effect between nitrogen rate and planting density. N × D × S: interaction effect between nitrogen rate, planting density, and season. * represents significance at $p < 0.05$, ** represents significance at $p < 0.01$, *** represents significance at $p < 0.001$, ns represents no significance.

3.1.2. Dry Matter Accumulation

In 2016–2017, the dry matter accumulation of perennial rice is shown in Figure 3. The dry matter of regrowth seasons (2016S, 2017F and 2017S) remained stable with the transplanting season (2016F), which was significantly affected by season ($p < 0.01$), nitrogen ($p < 0.001$) and density ($p < 0.01$) and interact effect of nitrogen and density ($p < 0.001$) (Table 1). When the N rate and planting density increased, the dry matter of leaf, stem and panicle increased. N2D3 showed the highest aboveground dry matter accumulation (15.46 t ha^{-1}) in four seasons (Table 1); the leaf, stem, and panicle weight were 1.67 , 5.34 and 8.45 t ha^{-1} , respectively, followed by N3D3 (15.15 t ha^{-1}). For the effect of N fertilizer, N1, N2 and N3 significantly improved aboveground dry matter accumulation (leaf, stem and grain weight) compared to N0. The increments were by 43.2%, 77.5% and 77.1%, respectively ($p < 0.05$). For the effect of planting density, the D3 and D2 significantly

increased the aboveground dry matter accumulation by 38.6% and 19% when compared to D1 ($p < 0.05$).

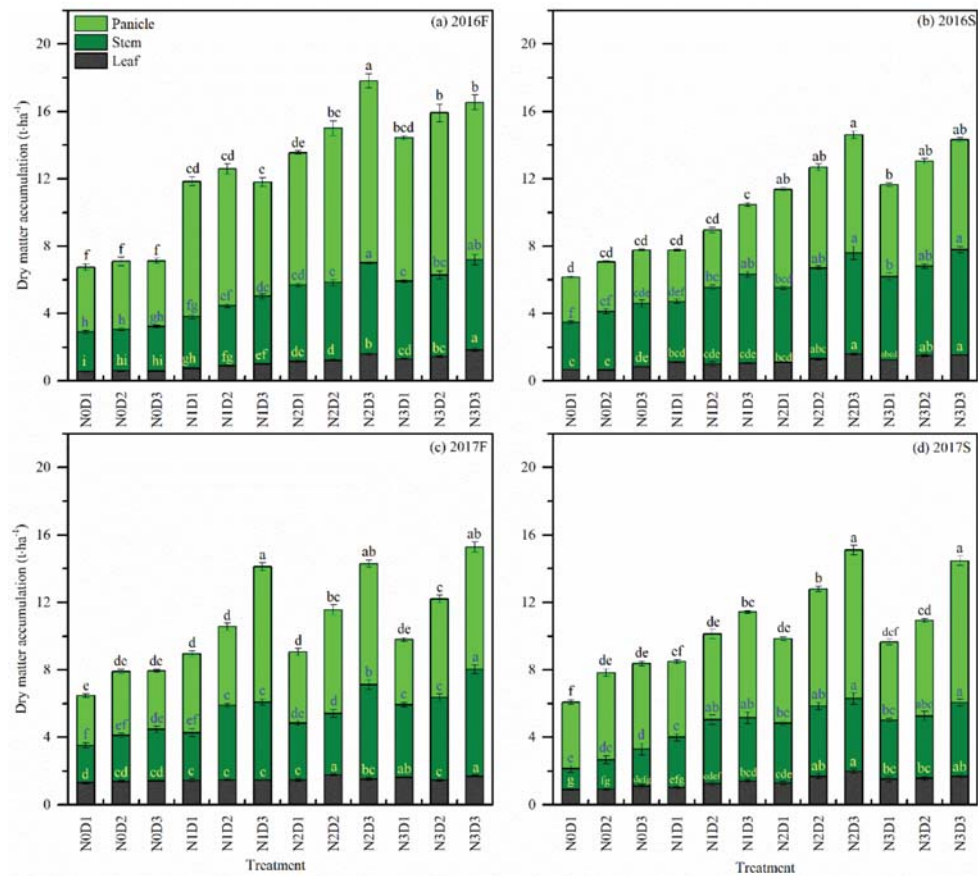


Figure 3. Dry matter accumulation of different treatments. (a) Dry matter accumulation in 2016F. (b) Dry matter accumulation in 2016S. (c) Dry matter accumulation in 2017F. (d) Dry matter accumulation in 2017S. Dry matter accumulation, including the dry matter of stem, leaf, and grain. 2016F, the first season of 2016 (transplanting season). 2016S, the second season of 2016 (regrowth season). 2017F, the first season of 2017 (regrowth season). 2017S, the second season of 2017 (regrowth season). Bars with different letters represent a significant difference at $p < 0.05$. The yellow letter represents the difference in the leaf. The purple letter represents the difference in the stem. The dark letter represents the branch and a difference in the panicle.

In the first season of 2016 and 2017, the panicle accounted for a large proportion of dry matter, which was 50.46–56.03%, and the straw (leaf and stem) accounted for 43.97–49.54% (Figure 3). In the second season (2016S, 2017S), the straw accounted for a large proportion of dry matter, which was 54.39–62.67%, and the panicle accounted for 37.33–45.61%.

3.2. Plant N Uptake

N rate and planting density significantly affected the N uptake of perennial rice ($p < 0.05$) (Figure 4); N uptake of perennial rice was stable in the first and second season, respectively. Compared to the second season (28.7–59.9%), perennial rice uptake and transfer of N in grain was higher in the first season (49.5–78.3%). The N uptake of grain accounted for 54.5–59.7% of aboveground plant N content and in 2016F, 2016S, 2017F and 2017S, these values were 73.5%, 50.6%, 65.1% and 37.9%, respectively. When the N rate and planting density increased, N uptake by stem, leaf and grain increased (Figure 4). For the N uptake by grain, N0, N1, N2 and N3 were 43, 73, 95 and 95 kg ha⁻¹, respectively and D1, D2 and D3 were 66, 74 and 89 kg ha⁻¹, respectively. For the N uptake by stem, N3 and D3 showed the highest value, 57 and 55 kg ha⁻¹, respectively. N uptake by leaf, N3, and D3

showed the highest value, 18 and 16 kg ha⁻¹. N3D3 and N2D3 showed the highest averaged N uptake values across the four seasons, which were 204 and 201 kg ha⁻¹, respectively.

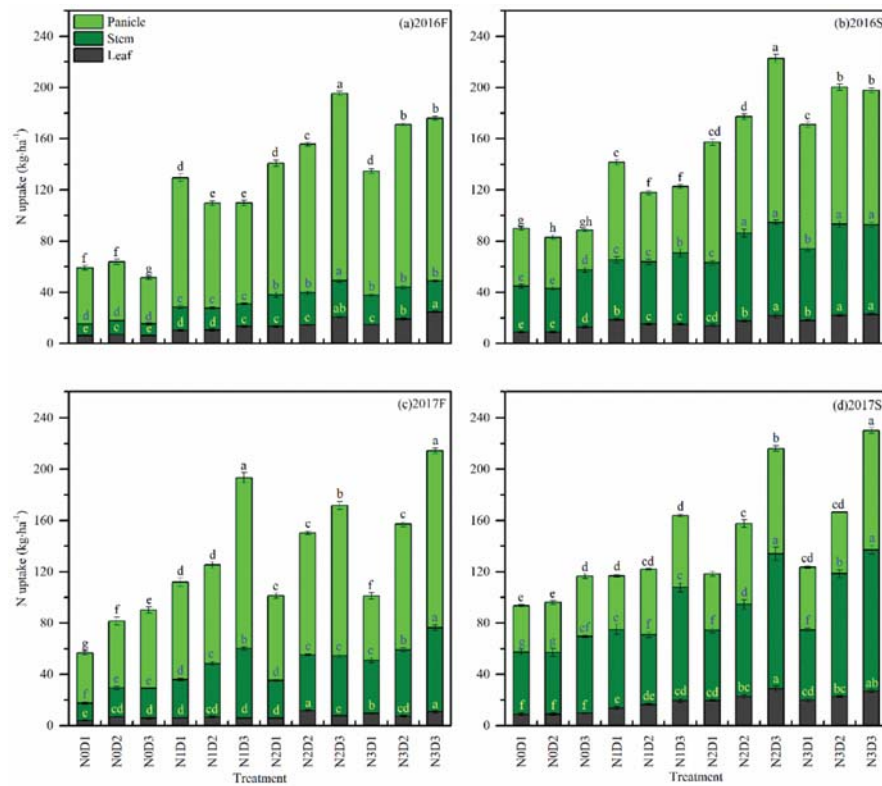


Figure 4. N uptake of aboveground dry matter. (a) N uptake in 2016F. (b) N uptake in 2016S. (c) N uptake in 2017F. (d) N uptake in 2017S. Plant N uptake, including the N uptake of stem, leaf, and grain. 2016F, the first season of 2016 (transplanting season). 2016S, the second season of 2016 (regrowth season). 2017F, the first season of 2017 (regrowth season). 2017S, the second season of 2017 (regrowth season). Bars with different letters represent a significant difference at $p < 0.05$. The yellow letter represents a difference in the leaf. The purple letter represents the difference in the stem. The dark letter represents the difference in the panicle.

After accounting for all treatments, the dry mater, straw (stem and leaf) and grain yield were significantly and positively related to the N uptake ($p < 0.01$) (Figure 5). The high N uptake of grain, straw yield and dry matter in N2D3 and N3D3 resulted in high dry matter and grain yield.

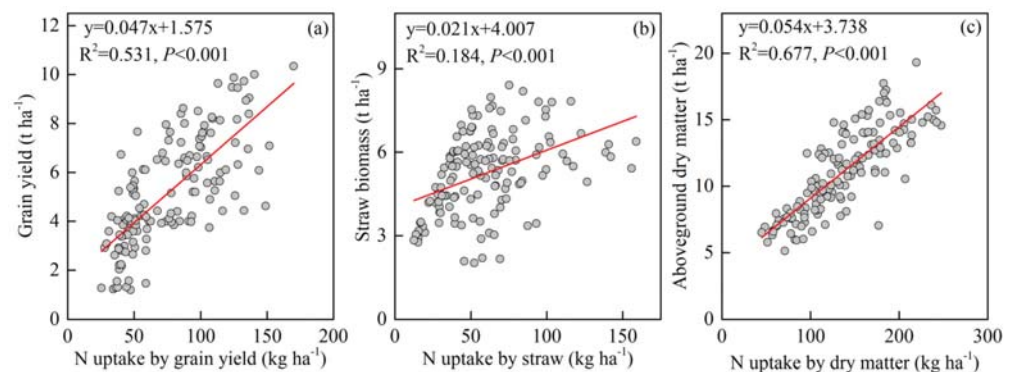


Figure 5. The relationship of N uptake with grain yield, straw biomass, and aboveground dry matter. (a) Relationship of N uptake by grain and grain yield. (b) N uptake by straw (stem and leaf) and straw biomass. (c) Relationship of N uptake by dry matter and aboveground dry matter.

3.3. Soil N Cycle

3.3.1. Soil N

In the four seasons, the soil N was significantly affected by season ($p < 0.001$) and the interaction effects of season. The interaction effect of season, N rate with planting density ($p < 0.001$) and N rate with planting density ($p < 0.05$) significantly affected the soil N (Table 2), neither N rate nor planting density had a significant effect on soil N (Figure 6). As the growth season continued, the soil N declined significantly ($p < 0.05$).

Table 2. N uptake and loss of perennial rice under different N rates and planting densities over four successive seasons of 2016–2017.

Treatment	N Uptake (kg ha ⁻¹)	N Loss (kg ha ⁻¹)	Soil N (g kg ⁻¹)
Season			
2016F	124.67 ± 47.33 a	98.42 ± 54.93 a	2.20 ± 0.05 a
2016S	147.33 ± 47.57 a	96.46 ± 56.88 a	2.14 ± 0.10 b
2017F	128.50 ± 48.85 a	104.81 ± 65.72 a	1.92 ± 0.07 c
2017S	143.50 ± 44.28 a	90.40 ± 68.74 a	1.83 ± 0.05 d
N rate			
N0	79.92 ± 19.10 d	12.29 ± 4.83 d	2.00 ± 0.17 a
N1	130.25 ± 24.93 c	93.52 ± 21.18 c	2.03 ± 0.18 a
N2	163.67 ± 35.65 b	109.67 ± 30.90 b	2.03 ± 0.17 a
N3	170.17 ± 37.68 a	171.60 ± 21.05 a	2.02 ± 0.17 a
Planting density			
D1	115.44 ± 42.45 c	109.31 ± 57.50 a	2.01 ± 0.17 a
D2	133.31 ± 40.93 b	100.67 ± 56.05 b	2.01 ± 0.16 a
D3	159.25 ± 41.59 a	82.58 ± 51.20 c	2.04 ± 0.17 a
ANOVA	F-value		
S (df = 3)	1.096 (ns)	0.987 (ns)	58.506 ***
N (df = 3)	38.063 ***	129.932 ***	0.612 (ns)
D (df = 2)	8.054 *	24.154 **	0.759 (ns)
N × S (df = 9)	3.514 *	5.008 **	0.876 (ns)
D × S (df = 6)	6.307 ***	1.616 (ns)	1.783 (ns)
N × D (df = 6)	7.758 ***	17.010 ***	2.673 *
N × D × S (df = 18)	2.585 **	2.289 **	4.560 ***

Different letters within a column represent significant differences at $p < 0.05$ (LSD). S: season. N: nitrogen rate. D: planting density. N × S: interaction effect between nitrogen rate and season. D × S: interaction effect between planting density and season. N × D: interaction effect between nitrogen rate and planting density. N × D × S: interaction effect between nitrogen rate, planting density, and season. * represents significance at $p < 0.05$, ** represents significance at $p < 0.01$, *** represents significance at $p < 0.001$, ns represents no significance.

3.3.2. Soil N Removal and Loss

In the perennial rice cropping system, soil N is mainly taken by the plant removal (N uptake by plants) (Figure 2b), and there were significant differences among the different treatments (Figure 7 and Table 2). With the increment in N rate, the N removal by perennial rice significantly increased ($p < 0.05$) and N0, N1, N2 and N3 were 80, 130, 164 and 170 kg ha⁻¹, respectively, but there was no significance between N2 and N3 ($p < 0.05$). For different planting density, when the density increased, N removal by plants increased significantly ($p < 0.05$); D1, D2 and D3 were 154, 178 and 212 kg ha⁻¹, respectively. In the four seasons, N3D3 and N2D3 resulted in the highest N removal values, which were 204 and 201 kg ha⁻¹, respectively.

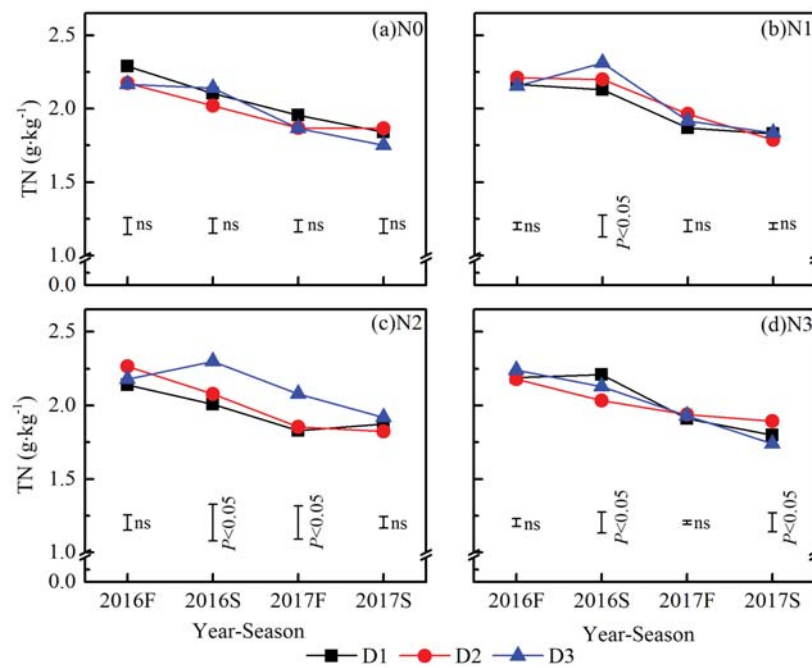


Figure 6. Soil total nitrogen (TN) of different treatments. (a) soil total nitrogen in 2016F. (b) soil total nitrogen in 2016S. (c) soil total nitrogen in 2017F. (d) soil total nitrogen in 2017S. 2016F, the first season of 2016 (transplanting season). 2016S, the second season of 2016 (regrowth season). 2017F, the first season of 2017 (regrowth season). 2017S, the second season of 2017 (regrowth season). Vertical bars represent the standard error for different treatments. $p < 0.05$ represent a significant difference among other therapies, and ns mean no difference among treatments.

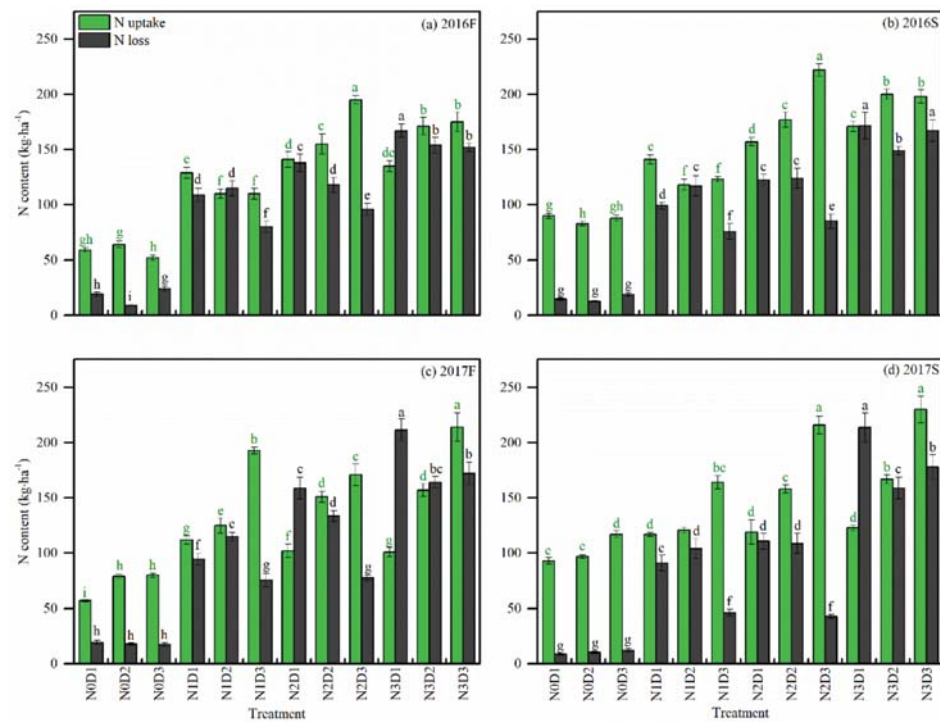


Figure 7. N removal by plants and soil N loss in the perennial rice cropping system. (a) N removal and soil N loss in 2016F. (b) N removal and soil N loss in 2016S. (c) N removal and soil N loss in 2017F. (d) N removal and soil N loss in 2017S. Bars with different letters represent significant differences at $p < 0.05$. The green letter represents the difference in N uptake. The dark letter represents a difference in N loss.

Different from the N removal by plants, soil N loss and loss rate increased with the increase in N rate and decrease in planting density (Figure 7 and Table 2). The soil N losses in N0, N1, N2 and N3 were 15, 94, 110 and 172 kg ha⁻¹, respectively, but there was no significance between N1 and N2 ($p < 0.05$). The soil N loss rates of N0, N1, N2 and N3 were 16.8%, 41.8%, 40.3% and 50.6%, respectively, while soil N loss in D1, D2 and D3 were 146, 134 and 110 kg ha⁻¹, respectively. The soil N loss rate of D1, D2 and D3 were 57.3%, 50.9% and 41.3%, respectively. High planting density significantly reduced soil N loss ($p < 0.05$). N3D1 resulted in the highest soil N loss and loss rate, which was 191 kg ha⁻¹ and 59.1%, respectively, and N0D2 resulted in the lowest value, which was 12 kg ha⁻¹ and 13.3%, respectively (Figures 7 and 8d).

3.3.3. Apparent N Balance

Soil apparent N balance was calculated by the difference between soil N input and soil N removal. In the perennial rice cropping system, soil N input includes N fertilizer application and decomposition of rice stubble (Figure 2b). The N input by rice stubble is mainly related to the N rate in straw and the biomass of straw. A high N rate and planting density would lead to high N input for perennial rice (Figure 8c). In the four seasons, N input by stubble of N0D1, N0D2, N0D3, N1D1, N1D2, N1D3, N2D1, N2D2, N2D3, N3D1, N3D2 and N3D3 were 8.4, 9.2, 10.8, 12.9, 13.2, 16.9, 13.1, 17.3, 20.8, 14.9, 19.7 and 22.2 kg ha⁻¹, respectively. According to the soil N input and soil N removal, soil N balance of N0D1, N0D2, N0D3, N1D1, N1D2, N1D3, N2D1, N2D2, N2D3, N3D1, N3D2 and N3D3 were -66.3, -71.6, -73.5, 8.1, 14.7, -10.6, 63.4, 37.0, -0.2, 122.3, 85.9 and 57.9 kg ha⁻¹, respectively (Figure 8e). In the four seasons, N2D3 achieved the soil N balance among all treatments.

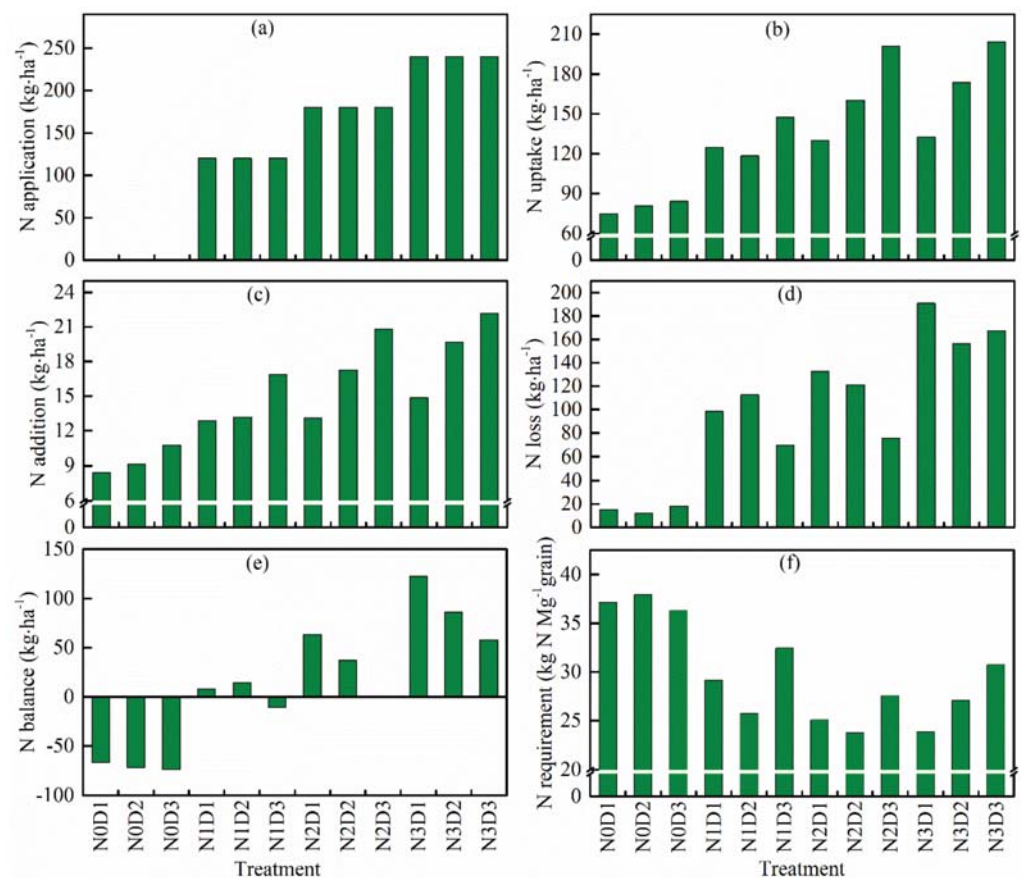


Figure 8. Soil N balance and N requirement under different N rates and plating densities in the perennial rice cropping system. (a) N application. (b) N uptake. (c) N addition. (d) N loss. (e) N balance. (f) N requirement.

3.4. N Effects and Requirement

N agronomic efficiency (NAE) and N recovery efficiency (NRE) are important indicators of the N fertilizer effect. With the increment in nitrogen, NAE and NRE increased and N2 resulted in better N effects (NRE: 46.5%, NAE: 22.2 kg N kg⁻¹) (Figure 9). D3 performed a better N effect for planting density, NRE was 55.9%, and NAE was 20.3 kg N kg⁻¹. In the four seasons, N2D3 resulted in the best N effect and NAE and NRE were 64.9 kg N kg⁻¹ and 26.5%, respectively.

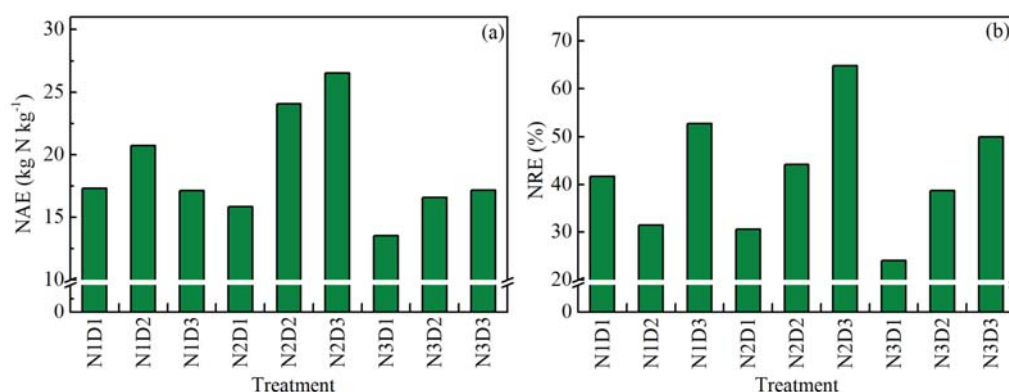


Figure 9. N agronomic efficiency and requirement under different N rates and plating densities in the perennial rice cropping system. (a) N agronomic efficiency (NAE) of other further additional treatments. (b) N recovery efficiency (NRE) of different treatments.

The N requirement refers to the amount of N required to produce 1 Mg of the rice grain, which is an important indicator to evaluate the N effect in perennial rice cropping system. In four seasons, the N requirement of perennial rice averaged 29.7 kg N Mg⁻¹ grain, and the N requirement of N0D1, N0D2, N0D3, N1D1, N1D2, N1D3, N2D1, N2D2, N2D3, N3D1, N3D2, and N3D3 were 37.1, 37.9, 36.3, 29.2, 25.7, 32.4, 25.1, 23.8, 27.6, 23.9, 27.1 and 30.7 kg N Mg⁻¹ grain, respectively (Figure 8f).

4. Discussion

4.1. Dry Matter Accumulation

Despite the high yield potential in the transplanting season, the sustainable dry matter and grain yield of perennial rice over regrowth seasons illustrated that perennial rice has a high and sustainable yield potential over the years (Table 1). Increasing fertilizer and planting density have been proposed as effective ways to improve rice yields [8,26]. When the N fertilizer and planting density increased, the grain yields increased to a certain extent [4,12]. In accordance with the annual rice, grain yield and dry matter accumulation of perennial rice showed the same response to N fertilizer and planting density (Figure 3 and Table 1). However, the improvement of fertilizer did not always result in a high crop yield, but sometimes low fertilizer use efficiency and more fertilizer runoff, thus causing a series of economic and environmental problems [27]. The more N fertilizer in N3 did not result in a significantly higher grain yield but it did result in more soil N loss and low N use efficiency (NAE and NRE) in the perennial rice cropping system. Additionally, N fertilizer and planting density often have an interaction effect on rice yield [15]; dry matter and grain yield of perennial rice are significantly affected by the interactional effect of N rate, planting density with the season, season with N rate and season with planting density. The proper N fertilizer rate and planting density in N2D3 are conducive to soil nitrogen absorption and crop production. The high N uptake in N2, N3, and D3 would lead to a high grain yield and dry matter accumulation by the positive relationship of N uptake with straw and grain yield (Figure 5). Although the N3 also resulted in a high grain yield and dry matter in four seasons as with N2, the high soil N loss and low N use efficiency would lead to high N erosion risk and less economic profit. Proper N application and planting

density could help to obtain a high grain yield and dry matter accumulation, improve N use efficiency and reduce soil N erosion [28]. The optimal combination of the N rate with planting density in N2D3 resulted from the highest dry matter accumulation and grain yield in a perennial rice cropping system.

4.2. *Plants N Uptake and N Use Efficiency*

N is the essential element for perennial rice production. Plant N uptake is closely related to dry matter accumulation and grain yield [29]. Recent literature reported that increasing crop nutrient uptake has emphasized the need for greater synchrony between crop nutrient demand and the nutrient supply from all sources throughout the growing season [30,31]. A proper high N rate could help plants absorb more N for production [32,33] and perennial rice should also show the same result. The N uptake of perennial rice significantly increased with the increase in N rate and planting density. N3D3 and N2D3 showed exceptionally high N uptake, but there was no significant difference between them. The N3 did not increase the N uptake of perennial rice but led to more soil N loss when compared with N2. Excessive N fertilizer input leads to luxury N absorption but also enhances soil N loss and leaching [10,11]. In four seasons, N uptake of perennial rice remained stable. In the first season, N uptake by plants was mainly transferred into grain yield, leading to a high grain yield of perennial rice. However, in the second season, more N was absorbed by straw, and then the grain yield was lower than that in the first season. The lower N uptake in the second season was one of the main reasons for the low yield of perennial rice.

In recent years, more and more fertilizer loss and pollution have appeared in the field by the desire for a higher crop yield, causing more environmental problems [12]. In China, the fertilizer use efficiency was 30–35%, which was far below that in the world [28]. So, we need to improve the N fertilizer use efficiency when pursuing a high crop yield. NAE and NRE were effective indicators in order to evaluate fertilizer use efficiency. Higher NAE and NRE values meant the fertilizer could produce higher grain yields and increase fertilizer use efficiency [34]. The high NAE and NRE in N2 and D3 stated that perennial rice could utilize N fertilizer efficiently in this nitrogen and planting density, resulting in the best N effect in the N2D3 mode.

The N requirement is also an effective indicator to evaluate the N fertilizer use efficiency and productivity, which refers to the N requirement to produce 1 Mg grain [23]. The low N requirement stated that working to the exact grain yield requires less fertilizer. The common N requirement in N2D3 indicated that N would produce a higher grain yield and have high and efficient use efficiency with less N loss and pollution in this mode. The highest NAE and NRE and proper N requirement in N2D3 also illustrated that the N fertilizer effect was the best in this mode. The perennial rice would produce a higher grain yield and less fertilizer loss and pollution and obtain more economic profit.

4.3. *N Cycle and Balance*

Soil N is the main soil nutrient for crop production. Soil N supply and balance immediately decided the crop productivity [35]. The soil N decreased as the experiment continued in the perennial rice field; this may be attributed to two reasons. First, the continuous high crop yield of perennial rice brought excessive nitrogen from the field, but the applied nitrogen could not compensate for this. Second, the no-till system with frequent irrigation in the perennial rice cropping system carried more nitrogen leaching and decomposition of soil organic matter. The N2D3 treatment reached the N balance of N input and output but decreased soil nitrogen in the field. This may be the increased N leaching carried by no-tillage with frequent irrigation. The majority of crop N came from the soil. If soil N was balanced in terms of inputs and outputs, the gaps between soil N consumption and fertilizer N replenishment would imply that other forms of exogenous N compensated for the soil N deficits, such as N deposition and biotic N fixation [36]. In the perennial rice cropping system, the source of soil N includes soil base N, N fertilizer

application, and N from some stubble decomposition, while the output of soil N includes N taken by plants and soil N loss. Maintaining soil N balance is the premise for sustainable rice production. In this study, the N2D3 mode resulted in almost soil N balance in the field. The minus N balance in N0 would lead to soil degradation and a reduction in crop yields. If exogenous N replenishment was lower than soil N consumption, it would hardly sustain the soil N supply capacity, eventually leading to soil fertility degradation and crop yield reductions [37,38]. In contrast, the high N balance in N3 would lead to surplus N and more soil N loss, which would result in serious environmental problems.

5. Conclusions

Studying the N utilization and N cycle in the perennial rice cropping system helps us to evaluate the N effects and soil N loss and formulate optimal N management for sustainable perennial rice production. In this study, the N2D3 mode resulted in a higher and more sustainable grain yield and dry matter accumulation with better N effects (NAE and NRE). Additionally, perennial rice under N2D3 mode uptake more N nutrients from the soil and this resulted in less soil N loss that could maintain the apparent N balance. In the perennial rice cropping system, N2D3 (180 kg N ha⁻¹ integrated with 226 × 10³ plants ha⁻¹) mode was the optimal N dependent planting density for sustainable production and soil N balance with less soil N loss and pollution.

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Article

Performance, Economics and Potential Impact of Perennial Rice PR23 Relative to Annual Rice Cultivars at Multiple Locations in Yunnan Province of China

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Abstract: Perennial grain crops hold the promise of stabilizing fragile lands, while contributing grain and grazing in mixed farming systems. Recently, perennial rice was reported to successfully survive, regrow, and yield across a diverse range of environments in Southern China and Laos, with perennial rice PR23 being identified as a prime candidate for release to farmers. This paper reports the evaluation of PR23 for release, by (1) comparing its survival, regrowth, performance, and adaptation with preferred annual rices across nine ecological regions in southern Yunnan Province of China; (2) examining the economic costs and benefits of perennial versus annual rice there; and (3) discussing the evidence for the release of PR23 as a broadly adapted and acceptable cultivar for farmers. Overall, the grain yield of PR23 was similar to those of the preferred annual rice cultivars RD23 and HXR7, but the economic analysis indicated substantial labour savings for farmers by growing the perennial instead of the annual. PR23 was comparable to the annuals in phenology, plant height, grain yield, and grain size, and was acceptable in grain and cooking quality. Farmers were keen to grow it because of reduced costs and especially savings in labour. PR23 is proposed for release to farmers because of its comparable grain yields to annual rices, its acceptable grain and milling quality, its cost and labour savings, and the likely benefits to soil stability and ecological sustainability, along with more flexible farming systems.

Keywords: adaptation; cultivar release; genotype by environment interactions; grain quality; labour savings; perennial grain crops; performance; regrowth; survival; yield

1. Introduction

Perennial crops can regrow after normal harvest, and have been adopted as part of the global toolkit for climate change mitigation and food security in the long term [1,2]. The potential benefits of perennial crops in sustainable farming systems are now drawing the attention of scientific researchers and government officials, not only because of the likely positive ecological effects on landscape and biodiversity conservation, but also the likely significant economic benefits for smallholder farmers [3–6].

In particular, the rice-growing lands in Asia are largely threatened due to pressure on soil resources [1]. Thus, the development of high-yielding perennial rice cultivars would address the environmental limitations of annual rice while helping to feed the rapidly increasing human population.

With a successful wide hybrid being reported between the wild perennial rice *Oryza longistaminata* and the annual rice *Oryza sativa* [7], it was originally proposed that perennial rice should be developed in order to stabilize fragile upland farming systems. Greater understanding of the genetic architecture of perenniality [8,9] was obtained from the study of viable progeny from the wide hybrid segregating for perenniality [10,11]. This led to proposals to introgress additional traits from the wild perennial species into the annual cultivated rice germplasm, and to the perennial rice breeding programs at Yunnan Academy of Agricultural Sciences and Yunnan University.

Rice is one of the most important crops grown worldwide, so the opportunity for the successful development of perennial rice has great potential. Viable progeny from the wide-hybrid segregating for perenniality also acquired nematode resistance and drought tolerance from the wild species, through linkage drag [10,11]. For the development of perennial rice to stabilize the fragile soils of rice-based farming systems, perennial rice breeding using derivatives of the original wide-hybrid and research on the genetic control of perenniality in rice have been continued [1,8–11]. These efforts offer the opportunity not only for the commercial use of perennial rice, but also for further understanding of the genetic architecture of perenniality in rice.

A successful perennial rice breeding program has been established in the Yunnan Academy of Agricultural Sciences and Yunnan University, with the high-yielding and broadly-adapted experimental line PR23 recommended for pre-release testing under paddy conditions in southern China and Laos [12,13]. Consequently, this paper reports the field evaluation of PR23 in comparison with the main conventional rice cultivars in pre-release testing under paddy conditions in nine ecological regions of Yunnan Province in China, between 2011 and 2017. The objectives were: (1) to compare the survival, regrowth, field performance, and adaptation of perennial rice PR23 with two conventional rice varieties across nine ecological regions of Yunnan; (2) to consider the economic costs and benefits in cultivation of perennial rice relative to annual rice; and (3) to discuss evidence for the commercial release of PR23 as a high-yielding and broadly-adapted perennial rice cultivar for farmers in the Yunnan Province of China.

2. Materials and Methods

Three experiments were conducted in 45 site-year (Environment E) combinations in the Yunnan Province of China (Table 1). Eleven sites were used: Jinghong (21°59' N, 100°44' E), Xingping (24°02' N, 101°34' E), Dehong (24°26' N, 98°35' E), Menghai (21°58' N, 100°25' E), Menglian (22°33' N, 99°59' E), Mengzhe (21°57' N, 100°14' E), Wenshan (23°23' N, 104°13' E), Honghe (23°07' N, 102°40' E), Puer (22°45' N, 100°51' E), Lancang (22°26' N, 99°58' E), and Yiliang (24°58' N, 103°11' E). Minimum temperature was generally lower at the higher-altitude sites (Supplementary Table S1), with rainfall generally lower December to April, and higher May to November (Supplementary Table S2), according to long-term weather data.

2.1. Experiment 1

In Experiment 1, a randomized complete blocks design with three genotypes and three replicates was used at each site. Plot size was 4.0 × 5.0 m, with 0.2 m row spacing and 0.4 m between hills. Environments are indicated by their environment code; e.g., Jinghong in the first harvest season of 2011 is JH11F (Table 1).

The three genotypes (G) comprised two *Oryza sativa* cultivars (RD23 and HXR7), and one perennial rice hybrid (PR23) obtained from the cross between *Oryza sativa* cv. RD23 and *Oryza longistaminata* (Table 2). RD23 is a popular *Indica* lowland rice cultivar from Thailand, and is grown widely across south-east Asia because of its broad adaptation, high yield potential, good disease resistance, and high grain quality [14]. In contrast, *Oryza longistaminata* is a wild rhizomatous perennial with poor

agronomic characteristics which comes from swampy areas. The cross between the two species was made in 1997 to combine the perennial habit of *O. longistaminata* with the agronomic features, broad adaptation, and yield potential of RD23 [7,11,12] via iterative selection in segregating populations from F2 in 2003 to F10 in 2010. HXR7 is another locally popular *Indica* lowland rice cultivar grown widely by farmers in Yunnan Province due to its high grain yield and its exceptional grain quality. Further details of HXR7 and other Chinese cultivars are available from the China Rice Data Center (<http://www.ricedata.cn/variety/varis/>). At some sites, farmers substituted a local cultivar with reputedly similar genetic background due to local preference or for greater cold tolerance at higher altitude (Supplementary Table S3). Nevertheless, the substituted cultivars were similar in phenotypic characteristics to the designated cultivar they replaced, so for analytical purposes, were considered this consistent with the designated cultivar. The perennial rice derivative PR23 was not substituted in any environment. Genotypes are referred to by their genotype code (Table 2).

The basal soil fertility of the nine sites used in Experiment 1 is shown in Table 3. Each site received a basal dressing of 30, 30, and 30 kg ha⁻¹ of N, P, and K, respectively, and was established by transplanting from nearby seed beds. After harvest, stubble was cut to 10 cm, so regrowth was consistent. The perennial rice PR23 was allowed to regrow, while RD23 and HXR7 were replanted in each subsequent cycle (Table 1). Each site had access to irrigation, which was used to minimize any yield reduction resulting from any periods of rainfall deficit. Timings of key events were recorded in each environment (as indicated in Table 1), with field duration (days) being from transplanting in the initial crop or stubble cut-off in the ratoon crop to maturity. Plant survival, flowering time, plant height, and panicles per plant were recorded. Regrowth percent is the proportion of plant stand which regrew in subsequent crops. Grain yield and yield components were measured using a five-point sampling method in each location.

2.2. Experiment 2

In Experiment 2, the same three genotypes were evaluated in larger unreplicated plots of about 25.0 × 25.0 m, with similar row and plant spacing to Experiment 1, in order to evaluate the genotypes at smallholder field scale. These larger experiments were conducted at Jing Hong and Puer only (Table 1), with genotypes, management, and measurements being identical to Experiment 1.

2.3. Experiment 3

In Experiment 3, larger plots of PR23 measuring 1.0–13.0 ha in size were established for validation and official release purposes. The plantings took place from 2016 to 2017 in Mengzhe, Menghai, Menglian, and Xingping in southern Yunnan. Field management by farmers was based on the high-yield cultivation protocol devised for perennial rice by Yunnan University. Grain yield was estimated by header harvesting of these commercial areas and compared with results from Experiments 1 and 2.

2.4. Statistical Analysis

Yield data were extracted from single-site analyses in Experiment 1 and combined with data from Experiment 2, so that data for three genotypes (G) across 35 environments (E) were available for analysis. To test combinability over experiments, analyses were conducted for 3G × 23E (Experiment 1), 3G × 12E (Experiment 2), and 3G × 35E (Combined). G × E interactions were analysed using the pattern analysis tool in CropStat [15], using cluster analysis of the G × E matrix transformed by environment standardization, in order to understand genotype adaptation for breeding and variety evaluation [16]. An agglomerative hierarchical algorithm based on minimizing incremental sum of squares was used to cluster the transformed data [17]. In this paper, cluster analysis was used to identify environmental groupings for genotype × environment interaction, but the three individual genotypes were retained for G × E interpretation, as three is minimal for valid analysis [18]. Patterns of grain yield and other selected parameters were then examined for the three genotypes over environment

groups. Means were compared using l.s.d. with appropriate degrees of freedom for main effects and interactions [19].

2.5. Experiment 4 and Economic Analysis

Financial data related to cost of inputs, rice cooking quality, milling, and popularity were directly obtained via a survey (Experiment 4) that was distributed to 20 farmers in Experiment 1 in 2016 to 2017. Although this was a small sample, the results reflected the situation throughout the study area, where farmers generally faced similar prices and costs. However, variability of these parameters in time and space must be considered, and this was examined via analysis of variance [19]. The cost of inputs for rice production included diesel, water, fertilizer, pesticide, seed, and human labour required to perform arable farming related to crop production processes such as land preparation, sowing, transplanting, irrigating, spraying, and harvesting. Output and profit were calculated as follows:

$$\text{Output} = \text{Grain yield (kg)} \times \text{The unit price of grain (Yuan/kg)},$$

$$\text{Profit} = \text{Output (Yuan)} - \text{Input (Yuan)}.$$

Four parameters were obtained to assess cost–benefit ratios and returns to investment per unit of financial input and per unit of labour, as shown below:

$$\text{Cost-Benefit by Investment in Inputs} = \text{Output (Yuan)}/\text{Input (Yuan)},$$

$$\text{Cost-Benefit by Investment in Labour} = \text{Output (Yuan)}/\text{days of labour (Yuan)},$$

$$\text{Return to Investment from Inputs} = \text{Profit (Yuan)}/\text{Input (Yuan)}$$

$$\text{Return to Investment from Labour} = \text{Profit (Yuan)}/\text{days of labour (Yuan)}.$$

Means of the parameters were again compared using l.s.d. with appropriate degrees of freedom for main effects and interactions [19].

Table 1. The 35 environments used to discriminate the perennial rice genotypes.

Env	Expt	Site	Altitude (m)	Season	Year	Code	Sow Re-Sow	TP/Cut	Flower	Mature	Duration (d)	Regrowth PR23 (%)	Yield (t ha ⁻¹)
1	1	Jinghong	550	First	2016	JH16F	30 Jan	05 Mar	19 May	30 Jun	117	n.a.	5.78
2	1	Jinghong	550	Second	2016	JH16S	-	14 Jul	19 Sep	08 Nov	118	93.3	5.25
3	1	Jinghong	550	First	2017	JH17F	-	17 Jan	18 Apr	02 Jun	137	92.0	5.89
4	1	Jinghong	550	Second	2017	JH17S	-	30 Jun	04 Sep	20 Oct	110	88.6	4.81
5	1	Xingping	600	Second	2016	XP16S	12 Jun	20 Jul	26 Sep	06 Nov	110	n.a.	6.23
6	1	Xingping	600	First	2017	XP17F	-	19 Feb	11 May	15 Jun	117	85.3	5.35
7	1	Dehong	900	First	2016	DH16F	22 Apr	23 May	01 Aug	15 Sep	116	n.a.	6.25
8	1	Dehong	900	First	2017	DH17F	-	21 Feb	19 Jun	13 Aug	167	90.0	6.05
9	1	Mengzhe	1255	First	2016	MZ16F	23 Dec	03 Feb	01 Jun	11 Jul	160	n.a.	8.85
10	1	Mengzhe	1255	Second	2016	MZ16S	-	20 Jul	30 Sep	16 Nov	120	98.2	6.32
11	1	Mengzhe	1255	First	2017	MZ17F	-	17 Feb	11 Jun	11 Jul	145	93.3	7.32
12	1	Mengzhe	1255	Second	2017	MZ17S	-	12 Jul	22 Oct	25 Nov	136	90.0	5.62
13	1	Wenshang	1260	First	2016	WS16F	23 Apr	25 May	07 Aug	01 Sep	100	n.a.	6.42
14	1	Wenshang	1260	First	2017	WS17F	-	12 May	13 Aug	25 Sep	137	65.0	6.13
15	1	Honghe	1300	First	2016	HH16F	17 Mar	01 Apr	26 Jun	08 Aug	130	n.a.	5.15
16	1	Honghe	1300	First	2017	HH17F	-	14 Apr	02 Jun	18 Aug	127	92.0	5.15
17	1	Puer	1305	First	2015	PU15F	19 Feb	04 Apr	30 Jun	05 Aug	124	n.a.	5.67
18	1	Puer	1305	First	2016	PU16F	-	20 Feb	10 Jul	10 Aug	173	96.0	5.85
19	1	Puer	1305	First	2017	PU17F	-	22 Mar	20 Jun	05 Aug	137	85.0	6.41
20	1	Lancang	1150	First	2016	LC16F	15 Feb	13 Apr	04 Jul	15 Aug	125	n.a.	6.07
21	1	Lancang	1150	First	2017	LC17F	-	10 Apr	27 Jun	11 Aug	124	96.1	6.12
22	1	Yiliang	1600	First	2016	YL16F	15 Mar	20 Apr	22 Jul	26 Aug	129	n.a.	9.71
23	1	Yiliang	1600	First	2017	YL17F	-	28 Apr	15 Aug	18 Sep	144	80.3	8.89
24	2	Puer	1305	First	2011	PU11F	07 Mar	15 Apr	06 Jul	11 Aug	118	n.a.	7.18
25	2	Puer	1305	First	2012	PU12F	-	28 Mar	26 Jun	12 Aug	137	95.0	6.70
26	2	Puer	1305	First	2013	PU13F	-	23 Apr	15 Jul	20 Aug	150	91.0	6.49
27	2	Puer	1305	First	2015	PU15FA	03 Mar	04 Apr	28 Jun	05 Aug	141	n.a.	5.11
28	2	Puer	1305	First	2016	PU16FA	-	20 Feb	08 Jul	10 Aug	169	96.0	5.23
29	2	Puer	1305	First	2017	PU17FA	-	22 Apr	06 Jul	05 Aug	133	85.0	5.86
30	2	Jinghong	550	First	2011	JH11F	10 Jan	20 Feb	20 Apr	10 Jun	110	n.a.	5.72
31	2	Jinghong	550	Second	2011	JH11S	-	13 Jun	17 Aug	22 Oct	131	93.0	5.20
32	2	Jinghong	550	First	2012	JH12F	-	10 Feb	27 Apr	05 Jun	116	90.0	5.15
33	2	Jinghong	550	Second	2012	JH12S	27 Jun	14 Jul	12 Oct	16 Nov	125	n.a.	6.12
34	2	Jinghong	550	First	2013	JH13F	-	05 Feb	29 May	08 Jul	153	94.0	5.07
35	2	Jinghong	550	Second	2013	JH13S	-	01 Aug	11 Nov	05 Dec	126	88.0	5.03
36	3	Mengzhe	1255	First	2016	MZ16F	28 Dec	30 Jan	3 Jun	11 Jul	162	n.a.	10.9
37	3	Mengzhe	1255	Second	2016	MZ16S	-	18 Jul	27 Sep	20 Nov	125	98.2	6.6
38	3	Mengzhe	1255	First	2017	MZ17F	-	15 Feb	13 Jun	13 Jul	148	93.3	8.7
39	3	Mengzhe	1255	Second	2017	MZ17S	-	13 Jul	25 Oct	29 Nov	139	90.0	6.5
40	3	Mengzhe	1300	First	2017	MZ17F	18 Feb	31 Mar	25 Jun	10 Aug	132	n.a.	8.6

Table 1. Cont.

Env	Expt	Site	Altitude (m)	Season	Year	Code	Sow Re-Sow	TP/Cut	Flower	Mature	Duration (d)	Regrowth PR23 (%)	Yield (t ha ⁻¹)
41	3	Menghai	1300	Second	2017	MZ17S	-	10 Aug	10 Oct	12 Dec	124	91.5	5.1
42	3	Menglian	980	First	2017	MZ17F	26 Dec	3 Feb	15 May	25 Jul	142	n.a.	10.1
43	3	Menglian	980	Second	2017	MZ17S	-	25 Jul	28 Sep	8 Nov	136	94.5	6.3
44	3	Xingping	760	First	2017	MZ17F	20 Dec	20 Feb	26 May	2 Jul	132	n.a.	9.42
45	3	Xingping	760	Second	2017	MZ17S	-	2 Jul	23 Sep	2 Nov	123	95.2	4.82
mean											133	90.7	6.47
l.s.d.											19	15.0	0.83

Note: Env: environment; Expt: experiment; Code: environment code used in subsequent tables and figures to designate each environment according to its site year and season; Sow/Re-sow: dates of sowing or of re-sowing of annuals; TP/Cut: dates of transplanting for initial crops or of stubble cut-off for ratoon crops; Flower: date of flowering; Mature: date of maturity; Duration: field duration from TP/Cut to Mature; Regrowth%: percent of plant stand which regrew in subsequent crops; Yield: grain yield; Code in bold type is the first crop in the cycle at each site. l.s.d. is $p < 0.05$.

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Table 2. Genotypes evaluated in perennial rice experiments.

Number Cases	Genotype Code	Growth Habit	Crop Type	Rice Type	Adaptation Response	SW-TP (d)	TP-FL (d)	FL-MT (d)	Height (cm)	Regrowth (%)	Yield (t ha ⁻¹)
1 (35)	PR23	Perennial	Interspecific	<i>japonica</i>	I, RL	33	70	41	110	89.8	6.04
2 (35)	RD23	Annual	Improved cv	<i>indica</i>	I, N	46	72	34	109	n.a.	6.41
3 (35)	HXR7	Annual	Improved cv	<i>indica</i>	I, N	48	74	32	112	n.a.	5.90
Mean						42	72	36	111	n.a.	6.12
l.s.d.						6.3	6.3	6.3	4.6	5.0	0.28

Note: SW-TP: duration from sowing to transplanting or cut-off; TP-FL: duration from transplanting/cut-off to flowering; FL-MT: duration from flowering to maturity. Adaptation: I = Irrigated, RL = Rainfed lowland, N = Nutrient responsive. l.s.d. is $p < 0.05$.

Table 3. Characterisation of soils at nine sites in Yunnan Province, China.

Site	pH	SOM	Total N	Avail N	Avail P	Avail K
		(g kg ⁻¹)	(g kg ⁻¹)	(mg kg ⁻¹)	(mg kg ⁻¹)	(mg kg ⁻¹)
Jinghong	5.05	34.00	2.10	155.60	7.58	139.10
Xingping	5.35	30.20	1.41	112.40	12.34	109.15
Dehong	4.95	29.60	1.64	116.00	89.99	177.18
Mengzhe	5.23	31.75	1.35	162.89	17.16	120.78
Wenshang	5.34	29.70	1.40	120.12	13.24	111.21
Honghe	5.39	24.49	1.74	120.12	22.38	111.18
Puer	6.10	39.00	2.50	123.00	12.30	108.00
Lancang	5.78	29.72	1.35	120.13	10.35	110.21
Yiliang	7.81	33.95	1.47	158.00	18.16	222.00
Mean	5.67	29.39	1.52	132.75	16.96	147.80

Note: SOM: soil organic matter; Total N: total nitrogen; Avail N: available nitrogen; Avail P: available phosphorus; Exch K: exchangeable potassium.

3. Results

Throughout the duration of the study, long-term mean monthly maximum temperature was generally favourable at all sites, exceeding 30 °C only at Honghe in August and Jing Hong in February–March (Supplementary Table S1). In contrast, long-term mean monthly minimum temperature was below 15 °C for 3 months in Jing Hong (550 m), 4 months in Honghe (1300 m), 5 months in Wenshang and Dehong (900 and 1260 m), 6 months in Lancang and Mengzhe (1150 and 1255 m), and 7 months in Puer and Yiliang (1305 and 1600 m), respectively (Supplementary Table S2). Overall, Jinghong at the lowest altitude was warmest with higher evaporative demand, and Yiliang at the highest altitude was coldest with lower evaporative demand (Supplementary Table S1). Rainfall was higher in 2017 than 2016 at all sites, with December–April generally drier than May–November (Supplementary Table S2). Soils were generally mildly acidic and sufficient in soil organic matter, total N, and available N, P, and K (Table 3).

Data were available for G × E analysis from three genotypes at 23 environments (Experiment 1), 12 environments (Experiment 2), and 35 environments (Combined) (Table 1 and Supplementary Table S3). Site mean yield ranged from 4.81 to 9.71 t ha⁻¹, with yields in the first season generally higher than in the second season, and with yields gradually declining in successive crops (Table 1). Field duration ranged from 100 to 169 days, with longer durations generally at cooler, higher-altitude sites (Table 1). The three genotypes were quite similar in mean field duration and mean grain yield, averaging 108 days and 6.12 t ha⁻¹, respectively, but only PR23 was able to successfully regrow in subsequent seasons, averaging 89.8% regrowth over its 23 crops (Table 2).

Data were analysed separately for Experiments 1 and 2, as well as combined over all environments. In all three analyses, genotype main effects accounted for less than 5% of the total sum of squares, environment main effects accounted for more than 70% of the total sum of squares, while the genotype by environment interactions accounted for 11.4%, 17.3%, and 25.7% of the total sum of squares, for three genotypes by 12, 23, and 35 environments, respectively.

Membership of environment groupings from the three analyses is shown in Table 4, with groupings aligned by environment membership. Remarkably, groupings from the separate analyses are retained in the combined analysis, with two groups in combined (E58 and E56) being composed solely of groups from Experiment 1 (E38 and E36), one group in combined (E34) being composed solely of one group from Experiment 2 (E11), and the remainder combining groups from both Experiments 1 and 2. There were only 3 of 35 environments which were exceptions, as underlines in Table 4. Consequently, combined analysis was chosen for interpretation of the data.

Table 4. Membership of environment groups for Experiment 1(23), Experiment 2 (12) and Combined (35) analyses. Groupings from the separate analyses by individual experiment were retained in the combined analysis, with only three exceptions, as underlined.

Experiment 1 (23)	Experiment 2 (12)	Combined (35)
-	E11 (1)	E34 (1)
-	JH13F	JH13F
E35 (4)	E14 (2)	E59 (5)
PU17F, YL16F, YL17F, <u>JH17S</u>	JH12S, JH13S	JH12S, JH13S, PU17F, YL16F, YL17F
E38 (7)	-	E58 (7)
MZ16S, MZ17S, JH17F, XP17F, HH17F, PU15F, <u>JH16S</u>	-	MZ16S, MZ17S, JH17F, XP17F, HH17F, PU15F, <u>JH17S</u>
E36 (3)	-	E56 (3)
XP16S, PU16F, WS17F	-	XP16S, PU16F, WS17F
E37 (3)	E17 (2)	E63 (7)
JH16F, WS16F, DH17F	JH11S, PU15FA	JH11S, PU15FA, JH16F, WS16F, DH17F, <u>JH16S</u> , <u>HH16F</u>
E20 (1)	E18 (3)	E61 (4)
LC16F	JH12F, PU12F, PU13F	LC16F, JH12F, PU12F, PU13F
E21 (1)	E16 (3)	E57 (4)
LC17F	JH11F, PU16FA, PU17FA	JH11F, PU16FA, PU17FA, LC17F
E40 (4)	E1 (1)	E60 (4)
MZ16F, MZ17F, DH16F, <u>HH16F</u>	PU11F	PU11F, MZ16F, MZ17F, DH16F

Cluster analysis on environment-standardized residuals was used to identify six environment groups for the three genotypes, which preserved 95.8% of the $G \times E$ sum of squares. The cluster dendrogram for environments (Figure 1a) initially separated a set of 12 environments (Fusion 67) from the other 23 environments (Fusion 68). Among the 12-environment set (Fusion 67), a group of four environments separated first (Environment group E60), then the remainder split into two groups of four environments (E61 and E57). Likewise, among the 23-environment set (Fusion 68), a group of six environments separated first (E62), then the remainder split into groups of seven and ten (E63 and E64), respectively. Membership of these groups is shown in Table 4, with E62 comprising E34 and E59, and E64 comprising E58 and E56. Although RD23 separated from PR23 and HXR7 in the cluster dendrogram for genotypes (Figure 1b), all three genotypes were retained for interpretation. Consequently, cluster analysis reduced the matrix from 3 genotypes \times 35 individual environments (=105) to 3 genotypes \times 6 environment groups (=18), whilst retaining the repeatable $G \times E$ variation (95.8%) for interpretation.

Grain yields, growth durations and regrowth percentages are shown for all three genotypes across each of six environmental groups in Tables 5–7, respectively. On average, grain yields were highest (7.40 t ha^{-1}) in E60 (PU11F, MZ16F, MZ17F, DH16F) and lowest (5.66 t ha^{-1}) in E64 (ten sites), E63 (seven sites), and E57 (four sites) (Table 5). RD23 yielded 6.41 t ha^{-1} on average, was highest yielding in E62, E64, and E63, and was lowest yielding in E61 and E60. HXR7 yielded 5.90 t ha^{-1} on average, was highest yielding in E61 and E57, but lowest in E64 and E63. In contrast, PR23 was more stable in grain yield, averaging 6.04 t ha^{-1} , and was generally intermediate in yield, except in E62 and E60, where it ranked third and first, respectively. On average, growth duration was longest at E60, where yields were highest (Table 6). HXR7 was longer in growth duration (151–171 days), RD23 was intermediate (145–161 days), and PR23 was shortest in growth duration (137–147 days), except in E60, where PR23 took 163 days and was highest yielding (8.49 t ha^{-1}). PR23 successfully regrew in all six environment groups, whereas RD23 and HXR7 did not (Table 7).

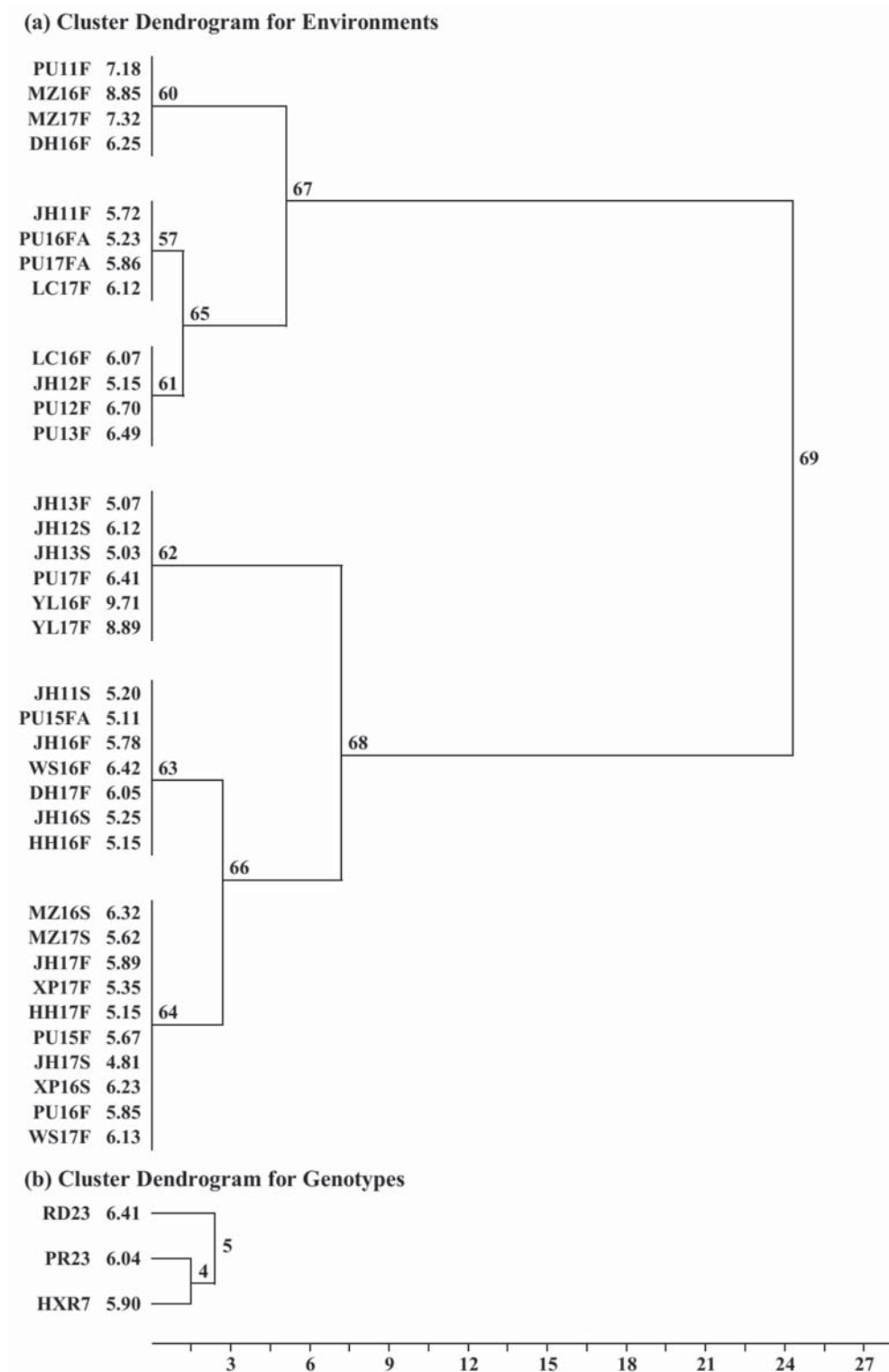


Figure 1. (a) Environment and (b) genotype groupings applied to standardized yield data for perennial rice PR23, and annual rice RD23 and HXR7, over 35 environments. The dendrograms show fusion levels at which the groups join. The fusion level is proportional to the increase in within-group sum of squares at each fusion. The 35 environments were truncated to six environment groups using Ward’s agglomerative clustering algorithm. Refer to Tables 1 and 2 for environment and genotype codes. Mean grain yields (t ha⁻¹) are also shown for each environment and genotype.

Table 5. Performance of three genotypes across six environment groups: grain yield ($t\ ha^{-1}$).

Genotype	E62 (6)	E64 (10)	E63 (7)	E61 (4)	E57 (4)	E60 (4)	Mean (35)	<i>l.s.d.</i>
G1-PR23	6.40	5.20	5.84	6.09	5.45	8.49	6.04	
G2-RD23	7.15	6.81	6.07	5.83	5.54	6.39	6.41	0.28
G3-HXR7	7.06	5.10	4.78	6.39	6.22	7.33	5.90	
Mean	6.87	5.70	5.56	6.10	5.73	7.40	6.12	
<i>l.s.d.</i>			0.48					0.68

Environment group codes are as in Figure 1a; *l.s.d.* are provided in each table for genotype, environment, and $G \times E$ for each trait ($p < 0.05$).

Table 6. Performance of three genotypes across six environment groups: field duration from transplant/cut to mature (days).

Genotype	E62 (6)	E64 (10)	E63 (7)	E61 (4)	E57 (4)	E60 (4)	Mean (35)	<i>l.s.d.</i>
G1-PR23	135	129	127	127	135	134	131	
G2-RD23	119	116	123	119	112	119	118	6.3
G3-HXR7	112	111	113	110	114	133	116	
Mean	122	119	121	119	120	129	122	
<i>l.s.d.</i>			10.9					15.4

Environment group codes are as in Figure 1a; *l.s.d.* are provided in each table for genotype, environment, and $G \times E$ for each trait ($p < 0.05$).

Table 7. Performance of three genotypes across six environment groups: regrowth percent (%).

Genotype	E62 (6)	E64 (10)	E63 (7)	E61 (4)	E57 (4)	E60 (4)	Mean (35)	<i>l.s.d.</i>
G1-PR23	86.8	88.4	92.1	92.0	92.4	93.3	89.9	
G2-RD23	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
G3-HXR7	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Mean	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	
<i>l.s.d.</i>			8.7					n.a.

Environment group codes are as in Figure 1a; *l.s.d.* are provided in each table for genotype, environment, and $G \times E$ for each trait ($p < 0.05$).

Cost-benefit analysis of perennial and annual rice across eight locations in Yunnan in Experiment 1 was compared by location (Table 8) and by growth habit and season (Table 9). Although locations did not differ significantly in cost-benefit per unit of investment, cost-benefit per unit of labour, or profit per unit of investment, locations did differ significantly in profit per day (Table 8), with Yiliang (226 Yuan/d) being the most profitable, and Puer the least profitable (118.5 Yuan/d). In contrast, all four parameters were statistically significant for the interaction between growth habit and season (Table 9). In each case, the ratoon crop of PPR23 was more profitable than the re-sown crop of HXR7 in the second season. As a consequence, the second crop was more profitable than the first, and PR23 was more profitable than HXR7 on average. Thus, allowing the perennial rice PR23 to ratoon resulted in greater profit, especially per unit of labour, due to substantial savings in the amount and cost of labour.

Different traits of perennial rice PR23 and annual rice RD23 and HXR7 are presented in Table 10. The grain yield of PR23 ($7.05\ t\ ha^{-1}$) was significantly higher than RD23 ($5.69\ t\ ha^{-1}$) and HXR7 ($5.89\ t\ ha^{-1}$) in Experiment 1 in both seasons. The major causes for this result were the lower number of panicles and the higher 1000-grain weight of PR23 in comparison with RD23 and HXR7. However, the number of spikelets per panicle of PR23 was slightly fewer than those of RD23 and HXR7. The growth duration of PR23 (135 d) was shorter than RD23 (152 d) and HXR7 (152 d) in the second season, though they were similar in the first season (157 d). Panicle length of PR23 (20.0 cm) was less than RD23 (25.4 cm) and HXR7 (22.9 cm) in both seasons. There was no significant difference in plant height. The duration of flowering in PR23 was longer than RD23 and HXR7 in both seasons, which may be

conducive to adequate pollination and fertilization in PR23. Grain quality of PR23 was similar to RD23, although it ranked behind HXR7, which farmers prefer. Nevertheless, the cooking quality of PR23 was comparable with HXR7, and higher than RD23. In addition, PR23 was preferred by millers due to its high rice yield and high milling percentage (73%). Overall, farmers preferred PR23 due to the savings of labour and decreased intensity of labour, as a result of not having to till and replant each season. Thus, PR23 had obvious economic benefits, resulting in its growing popularity with farmers.

Finally, perennial rice PR23 was successfully grown and mechanically harvested from four large demonstration areas of 1.0 to 13.0 ha on-farm in southern Yunnan (Table 11). Total grain yield of PR23 per year exceeded 13 t/ha in each demonstration area, with Mengzhe yielding 17.4 t ha⁻¹ in 2006 from seasons 1 and 2, and 15.1 t ha⁻¹ in 2017 from seasons 3 and 4. Ratoon percentage of PR23 ranged from 90.0–98.2%, including 93.3% and 90.0% in seasons 3 and 4 at Mengzhe, indicating its strong perenniality across a range of irrigated environments. Grain yield of PR23 was higher in the first season than in the second season, due to the shorter growth duration, fewer panicles, and fewer spikelets per panicle in the second season. These results confirmed that PR23 produced high yield, excellent regrowth, and adaptability when grown at commercial scale on-farm. Consequently, there has been an upsurge in demand for PR23 among local subsistence farmers and large commercial growers, indicating a bright future for perennial rice production and application across wider areas. This evidence is consistent with the need to release PR23 to farmers in Yunnan, as the first-ever perennial rice grain crop.

Table 8. Economic analysis of perennial and annual rice cropping at each of eight locations in southern Yunnan Province of China, ** $p < 0.01$.

Parameter	Dehong	Honghe	Jinghong	Lancang	Mengzhe	Puer	Wenshan	Yiliang	Mean	I.s.d.
C-B/Yuan	0.597	0.399	0.311	0.283	0.384	0.200	0.338	0.603	0.389	0.348 n.s.
C-B/Day	69.7	40.2	42.7	28.8	41.3	20.9	34.4	84.2	45.3	46.24 n.s.
Profit/Yuan	1.597	1.399	1.311	1.283	1.384	1.200	1.338	1.603	1.389	0.348 n.s.
Profit/Day	178.3	138.5	172.7	127.2	147.3	118.5	133.0	226.4	155.2	47.55 **

Cost-benefit per unit of investment (C-B/Yuan), cost-benefit per unit of Labour (C-B/Day), profit per unit of investment (Profit/Yuan), and profit per unit of labour (Profit/Day).

Table 9. Economic analysis of perennial and annual rice cropping for perennial rice PR23 and annual rice HXR7 in original and ratoon crops, averaged over eight locations. ** $p < 0.01$.

Season	C-B/yuan		C-B/day		C-B/day		Profit/y		Profit/d		Profit/d	
	PR23	HXR7	Mean	PR23	HXR7	Mean	PR23	HXR7	Mean	PR23	HXR7	Mean
Original	0.293	0.178	0.235	32.8	19.9	26.3	1.293	1.178	1.235	141.5	127.7	134.6
Ratoon	0.972	0.114	0.543	115.9	12.4	64.2	1.972	1.114	1.543	232.5	119.3	175.9
Mean	0.633	0.146	0.389	74.4	16.2	45.3	1.633	1.146	1.389	187.0	123.5	155.3
Genotype	G × S		G × S		G × S		Genotype		Genotype		G × S	
I.s.d.	0.174 **	0.174 **	0.246 **	23.12 **	23.12 **	32.70 **	0.174 **	0.174 **	0.246 **	23.78 **	23.78 **	33.63 **

Table 10. Traits of PR23, RD23 and HXR7 in Experiment 1. I.s.d. are $p < 0.05$.

Trait	Season	PR23	RD23	HXR7	Mean	Source	I.s.d.
Sowing–Transplanting (d)	1	37	40	42	40	S, G ^a	6.3
	2	n.a.	39	41	40	S × G	8.9
T'plant/Cut-off–Flower (d)	1	84	85	80	83	S, G	6.3
	2	90	78	78	82	S × G	8.9
Flower–Mature (d)	1	39	34	38	37	S, G	6.3
	2	46	36	36	40	S × G	8.9
Plant height (cm)	1	109	109	115	111	S, G	4.6
	2	111	107	113	111	S × G	6.5
Panicle length (cm)	1	20.9	25.6	23.3	23.3	S, G	0.6
	2	19.1	25.1	22.5	22.2	S × G	0.8
Effective panicles (10 ⁶ ha ^{−1})	1	2.90	2.40	2.42	2.57	S, G	0.15
	2	3.00	2.20	2.26	2.49	S × G	0.21
Spikelets/panicle (no)	1	139	152	147	146	S, G	7.26
	2	121	149	142	137	S × G	10.26
Grains/spikelet (no)	1	66.8	61.9	65.7	64.9	S, G	2.43
	2	61.9	69.9	63.2	64.0	S × G	3.43
1000-Grain Weight (g)	1	26.2	25.2	25.2	25.5	S, G	0.44
	2	25.5	24.4	24.7	24.9	S × G	0.62
Grain yield	1	7.05	5.69	5.89	6.21	S, G	0.28
	2	5.73	5.59	5.01	5.44	S × G	0.39
Grain quality *	1	2	2	1	n.a.	S, G	n.a.
	2	2	2	1	n.a.	S × G	n.a.
Cooking Quality *	1	1	2	1	n.a.	S, G	n.a.
	2	2	2	2	n.a.	S × G	n.a.
Farmer preference **	1	2	3	1	n.a.	S, G	n.a.
	2	2	3	1	n.a.	S × G	n.a.
Miller preference **	1	1	2	2	n.a.	S, G	n.a.
	2	1	2	2	n.a.	S × G	n.a.
Regrowth	1	n.a.	n.a.	n.a.	n.a.	S, G	5.0
	2	87.0	n.a.	n.a.	n.a.	S × G	n.a.

I.s.d. for site, genotype and site × genotype (S × G) are shown for each trait ($p < 0.05$): * 1 = good, 2 = medium, 3 = ordinary ** 1 = much, 2 = better, 3 = general.

Table 11. Demonstration of PR23 in large plots for four locations. The first crop of the cycle is shown in bold. I.s.d. are $p < 0.05$.

Year	Season	Sites	Area (ha)	No. of Grain Panicle ($\times 10^6/\text{ha}$)	Spikelets per Panicle	Seeds Setting Rate (%)	1000-Grain Weight (g)	Ratoon (%)	Grain Yield (t/ha)	Total Seasons 1&2
2016	1	Mengzhe	1	3.3	138.1	90.7	26.0	-	10.9	
2016	2	Mengzhe	1	2.9	110.2	82.9	24.8	98.2	6.6	17.4
2017	1	Mengzhe	1	4.5	108.7	80.1	21.9	93.3	8.7	
2017	2	Mengzhe	1	3.1	108.6	78.8	25.7	90.0	6.5	15.1
2017	1	Menghai	13	3.3	109.4	75.2	22.8	-	8.6	
2017	2	Menghai	13	3.4	64.1	74.6	26.8	91.5	5.1	13.7
2017	1	Menglian	2.33	3.5	141.8	86.0	23.2	-	10.1	
2017	2	Menglian	2.33	3.4	139.8	70.3	24.3	94.5	6.3	16.4
2017	1	Xingping	8	3.2	135.7	82.1	23.6	-	9.4	
2017	2	Xingping	8	2.9	92.7	94.5	23.7	95.2	4.8	14.2
Site ^a				0.82	30.7	14.7	3.2	8.7	1.0	2.0
Season				0.52	19.4	9.3	2.0	n.a.	0.6	1.2
S \times S				1.16	43.4	20.7	4.6	n.a.	1.3	2.6

^a I.s.d. for site, season and site \times season (S \times S) are shown below the table for each trait ($p < 0.05$).

4. Discussion

4.1. Survival, Regrowth, Performance, and Adaptation of PR23 versus Preferred Annual Rices

The performance of perennial rice (PR23) relative to two popular annual rice cultivars (RD23 and HXR7) was examined across 35 environments in Yunnan Province of China, with cluster analysis confirming the validity of this combined analysis over experiments 1 and 2 (Table 4). On average, the three genotypes were quite similar (Table 2), which is not surprising since all three genotypes were considered to be well-adapted from previous evidence [12,13]. Nevertheless, the $G \times E$ interaction accounted for 25.7% of the total sum of squares in the combined analysis of variance, while cluster analysis identified six environmental groups from the 35 environments (Figure 1), which retained 95.8% of the $G \times E$ sum of squares.

While genotype mean yields were similar on average, the rankings changed among environmental groups (Table 5). In environmental groups E62, E63, and E64 (Fusion 68), RD23 was highest yielding on average (6.68 t ha^{-1}), while in E60, E61, and E57 (Fusion 68), PR23 or HXR7 were highest yielding (Figure 1 and Table 5).

Environment group E60 was the highest yielding on average (7.40 t ha^{-1}), with PR23 performing best there (8.49 t ha^{-1}). The four environments in E60 (Table 4) were all first-season, mostly first crops in the cycle, and at altitudes of 900–1300 m (Table 1). This suggested PR23 had a higher yield potential in the first crop (also evident in Table 10), perhaps due to a higher seedling vigour in the interspecific hybrid, as shown by its reduced time in the seedling nursery up to transplanting (Table 2). Higher altitude and cooler temperature would also favour a high yield potential there. HXR7 was highest yielding in environmental groups E61 and E57 (Table 5), which featured predominately later-cycle crops (second and third crops; Table 1) and substitute cultivars for HXR7, especially in E61 (Supplementary Table S3). The slightly lower yield of PR23 in E61 and E57 could be associated with ratoon crops of the perennial (also evident in Table 10), while HXR7 may have benefited from farmer selection of locally-adapted cultivars—especially in E61.

Conversely, in environment groups E63, E64, and E62 (where RD23 was highest yielding), its performance would also have benefited from farmer selection of locally-adapted cultivars, which occurred in most of these environments (Supplementary Table S3). Given that the comparison is always among well-adapted genotypes, it is not surprising that such changes can alter the rankings within an environment group. However, it must be emphasized that all in cases, grain yields were universally high, again emphasizing the broad adaptation of PR23 relative to leading popular cultivars, and even locally preferred cultivars at individual locations. These data suggest that PR23 can be grown successfully across this range of environments, though it can be slightly exceeded at individual locations by a locally-preferred genotype. Nevertheless, PR23 would be a good choice at all locations tested.

Interestingly, the effects of cooler temperatures were less apparent in this data set than in previous reports [12]. This appears to be due to improved management, with times of sowing and resowing in the nursery (under cover for warmth during seedling establishment), allowing growth after transplanting (annual rices RD23 and HXR7) or regrowth after cut-off (perennial rice PR23) to avoid coincidence of sensitive growth stages with temperatures below $15 \text{ }^{\circ}\text{C}$ (Supplementary Table S1 and Table 1). Likewise, with irrigation, and in the absence of lower latitude sites with higher evaporative demand [13], rainfall deficit was not an issue here. As a result, the grain yields recorded here were generally much higher than in previous reports [12,13].

The major difference between genotypes was in capacity for regrowth, with PR23 able to regrow at every location in every environmental group. In contrast, RD23, HXR7, and the substitute genotypes were universally poor in regrowth, lacking in vigour, and failing to contribute grain from any border sections not resown as intended. Phenology was generally quite similar among the three genotypes overall, although sowing to transplanting was less in PR23, allowing it a little extra time in flowering

duration and grain filling (Tables 2 and 6). The three genotypes were also similar in plant height (Table 2).

Importantly, the evidence in Table 11 clearly confirms the transferability of perennial rice technology across scales from small experimental plots of 20 m² (Experiment 1) to smallholder fields of about 1 mu or 625 m² (Experiment 2), to large fields of 1.0 to 13.0 ha on commercial farms with header harvesting (Experiment 3). This is strong evidence supporting the need to release PR23 to farmers.

4.2. Economics and Farmer Preference of PR23 Perennial Rice versus Annual Rice Cultivars

The results from economic analysis demonstrate the economic advantages to the farmer of growing perennial rice, which accrue predominately via savings in labour and labour intensity by not having to sow and transplant in each crop cycle (Tables 8 and 9). Labour scarcity is increasingly an issue in rice production [20–22], so it is not surprising that farmers liked the capacity of PR23 to regrow after harvest (Table 10), thereby reducing labour demand, and also the drudgery implicit in transplanting, especially for women and children.

Consequently, the first preference of the farmers was for perenniality, as it saved labour and labour intensity by removing the need for tillage, sowing, and transplanting in subsequent crop cycles. Second, the grain yield of PR23 was stable and similar to those of the currently preferred annual rice cultivars (Table 10). Third, the farmers were happy with the grain, cooking, and milling quality of PR23 (Table 10). In addition, the farmers observed that PR23 was more tolerant of rice blast, which has caused serious damage in their rice fields, and is now included as a criterion for cultivar release by government.

It is important to note that the observed regrowth in PR23 was never less than 65% (Table 1), which was still sufficient to support a grain yield of 6.13 t ha⁻¹ at Wenshang 2017F. Further research is needed to determine a minimum regrowth percentage at which grain yield may be compromised, and hence, a further cycle of regrowth may become uneconomic. Nevertheless, the results presented here are consistent with the viability of up to a six-crop cycle, at least under the conditions of test. The results also suggest that a perennial rice, whilst retaining the advantages of ratooning a conventional rice cultivar for reduced costs [23], should accrue even greater benefit to the farmers, as a result of the sustained regrowth capacity in the perennial (Table 1).

4.3. The Case for Release for PR23 to Farmers

This paper clearly confirms the broad adaptation of PR23 at levels comparable to or better than popular annual rice cultivars RD23 and HXR7. Consistently high yields were attained by PR23 across sites, years, and cycles of regrowth, with the perennial habit, reduced labour requirement, and greater economic returns seen as major advantages. Grain quality was equal to RD23, and milling quality exceptional, so farmers and millers were happy with PR23. Consequently, we conclude that PR23 should be released to farmers because of its high yield performance, suitable quality, labour savings, economic advantages, and likely benefits to system flexibility and sustainability, as a result of the perennial growth habit.

Supplementary Materials: The following are available online at <http://www.mdpi.com/2071-1050/10/4/1086/s1>, Table S1: Long-term mean monthly maximum & minimum temperature (°C) & pan evaporation (mm) for 9 locations in Yunnan Province; Table S2: Monthly rainfall (mm) in 2016 and 2017 relative to the long-term mean monthly rainfall (mm) at 9 locations in Yunnan province; Table S3: Identities and mean grain yields (t ha⁻¹) of 3 genotypes in each of 35 environments in Yunnan Province.

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first draft under L.J.W. guidance; L.J.W. wrote manuscript; F.Y.H. conceived the research and provided guidance throughout the study.

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Genotype by environment interactions for grain yield of perennial rice derivatives (*Oryza sativa* L./*Oryza longistaminata*) in southern China and Laos



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ABSTRACT

Perennial grains have been proposed to stabilise fragile lands while contributing grain and grazing in mixed farming systems. Genotype by environment (G×E) interactions for grain yield were investigated in 22 perennial rice (*Oryza sativa* L./*Oryza longistaminata*) derivatives over four successive growing seasons at three sites in Yunnan in southern China and one site in Lao PDR. The G×E interaction accounted for 25.7% of the total sum of squares, with environment and genotype responsible for 57.4% and 16.9%, respectively. Cluster analysis identified seven environment and six genotype groups, which accounted for 55.6% of the G×E sum of squares. Principal component axes 1, 2 and 3 accounted for 42.3%, 19.1% and 16.5% of the G×E-SS, respectively, with PCA1 indicating yield potential, PCA2 delay in phenology under environmental stress, and PCA3 ratoon percentage. Environment groups differed in mean temperature, whether dry season or wet season, and occurrence of environmental stresses, such as periods of low minimum temperature or periods of rainfall deficit. Genotype groups differed in adaptation to these diverse environments. For genotype groups, G5 (PR23) was highest-yielding and broadly adapted across environments, while G1 (line 188, both 137s, both 139s, both 147s) was low-yielding and poorly adapted. Other genotype groups showed preferential adaptation: G3 (lines 60, 251, 264, Bt69, Bt71) to Simao/Dry Season (E3 and E4), G4 (lines 75, 243, 246, 249, 255) to Menglian/Wet Season (E1 and E2), G2 (line TZ) to Jing Hong 2013 (E7), and G6 (lines 56, 59, 214) to Jing Hong 2102 and Na Pok (E6 and E5). The results imply that regrowth success and maintenance of spikelet fertility over regrowth cycles are important for adaptation of perennial rice, especially to low minimum temperature at higher altitude and rainfall deficit at lower altitude, and future breeding programmes in perennial rice should address these environmental stresses. The high yield and broad adaptation of PR23 (G5) over environments makes it a prime candidate for release to stabilise fragile lands in the humid and subhumid tropics, while contributing grain and forage in mixed-farming systems.

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Abbreviations: G×E, genotype by environment interaction.

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1. Introduction

Global food security is under threat, due to rising global population, pressure on the resource base, and climate change. While the best lands (16.5 million km²) have soils of low to moderate risk of degradation and capable of sustaining high-yielding annual crops, more than 50% of world population relies on marginal lands (43.7 million km²), which are at high risk of degradation under annual cropping (Eswanan et al., 1999). For sustainable production, marginal lands in particular require agroecosystem consideration, to ensure their health and viability in the long term. Most likely, this requires maintenance of ground cover and biodiversity, so soil resources are retained in situ (Tilman et al., 2011). Perennial grains have been proposed to have an important role there (Glover et al., 2010), by stabilising land and soil resources, while contributing grain, grazing and forage in a mixed farming system, in conjunction with associated rangeland, pasture, forage, annual crops and vegetables. Livestock usually form part of the farming system on marginal lands, so integration of livestock with crop, pasture and forage should enhance farmer livelihood and system sustainability, and perennial crops can serve as both grain and forage (Bell et al., 2008; Pimentel et al., 2012). While the pressure is on the best lands to sustain the grain pool for food security under high-yielding irrigated crops, marginal lands can assist food security via system flexibility and diversity, with integrated crop-livestock systems. The intent is not to displace high-yielding annual grain crops from the best land, as that would require extra land be brought into cropping to compensate. Rather the intent is more efficient integrated systems for marginal lands, with dual-purpose perennial grains (Wade, 2014).

Research is underway to develop perennial versions of a number of annual grain crops (Batello et al., 2014), in order to facilitate the expected systems benefits. Two approaches are possible; either domestication of a perennial species, or wide hybridisation of the annual crop with a perennial relative. Domestication requires selection for agronomic type including non-shattering and larger grain size (Dehaan et al., 2014). Wide hybridisation, which requires embryo rescue in some instances, can be used to introgress desired characteristics such as perenniality into the annual crop germplasm pool, via selection for ratooning ability and sustained floret fertility (Cox et al., 2002). The development of perennial rice was proposed in order to stabilise fragile upland farming systems (Schmit, 1996). A successful wide hybrid between the annual rice *Oryza sativa* and the wild perennial rice *Oryza longistaminata* was reported (Tao and Sripichitt, 2000). Viable progeny from the wide-hybrid segregating for perenniality were created (Sacks et al., 2003, 2006), which allowed for greater understanding of the genetic architecture of perenniality (Hu et al., 2003, 2011), and proposals for additional traits that could be introgressed from the wild perennial species into the annual cultivated rice germplasm. Perennial rice breeding using derivatives of the original wide-hybrid and knowledge about the genetic control of perenniality in rice continues in Yunnan Academy of Agricultural Sciences and Yunnan University (Zhang et al., 2014).

This paper reports the first study of genotype by environment interactions for grain yield of perennial rice in the field, and the relationships between yield-related traits, using perennial rice derivatives from the cross between *O. sativa* and *O. longistaminata* (Tao and Sripichitt, 2000). Field experiments were conducted at three sites in Yunnan Province of China and one site in Lao PDR over two years, with the evaluation at each site potentially covering two successive dry and wet seasons. This initial set of derivatives was evaluated under rainfed lowland conditions with access to supplementary irrigation, which was available to assist survival under harsh dry season conditions if needed. The objectives were (1) to assess survival, regrowth and field performance of perennial rice

Table 1

The 12 environments used to discriminate perennial rice genotypes (l.s.d. = 0.34; P = 0.05).

Number	Site	Year	Season	Code	Yield (t ha ⁻¹)
1	Jing Hong	2012	Dry	J2D	6.04
2	Jing Hong	2012	Wet	J2W	2.05
3	Menglian	2012	Dry	M2D	3.07
4	Menglian	2012	Wet	M2W	4.06
5	Simao	2012	Dry	S2D	2.63
6	Na Pok	2012	Wet	N2W	0.94
7	Jing Hong	2013	Dry	J3D	2.23
8	Jing Hong	2013	Wet	J3W	1.17
9	Menglian	2013	Dry	M3D	3.15
10	Menglian	2013	Wet	M3W	1.79
11	Simao	2013	Dry	S3D	1.42
12	Na Pok	2013	Wet	N3W	1.93
	Mean				2.54

derivatives in up to four growing seasons in each of four locations, (2) to consider traits needed for successful adaptation to this target population of environments, and (3) to identify implications for selection, release and farmer livelihood.

2. Materials and methods

2.1. Planting location, experimental design and plot management

The experiments were conducted in 12 site-season-year (Environment E) combinations, at Jing Hong (21°59' N, 100°44' E, 611 m), Menglian (22°33' N, 99°59' E, 955 m) and Simao (22°79' N, 100°96' E, 1340 m) in Yunnan Province of southern China, and at Na Pok (17°57' N, 102°34' E, 171 m) in Vientiane Province of Lao PDR. Each of the four sites was continued for two years, 2012 and 2013, with the potential for up to two crops to be harvested each year, from the dry and wet seasons, respectively. While rice may ratoon or reshoot from basal nodes after harvest in suitable conditions (Douthwaite et al., 1995), ratoon potential is expected to be stronger in perennial rice derivatives being evaluated here. At each site, a randomised complete blocks design was used, comprising 22 genotypes with 2–3 replicates. Long-term weather data showed minimum temperatures were lower at the higher altitude sites in the north (Supplementary Table 1), especially at Simao, so only one dry season crop per year could be harvested there. Likewise, rainfall declined from Na Pok to Simao and Menglian to Jing Hong (Supplementary Table 2), but with a more pronounced difference between wet and dry seasons at Na Pok, which allowed only one wet season crop per year to be harvested there. Consequently, data were available for GxE analysis from a total of 12 Environments (Table 1), which for simplicity, are referred to by their environment code, e.g., Jing Hong in the dry season of 2012 is referred to as J2D.

The soil at Jing Hong had a pH of 4.6, organic C 24.7 g kg⁻¹, total N 1.37 g kg⁻¹, available P 15.3 mg kg⁻¹, exchangeable K 144.1 mg kg⁻¹. At Menglian, the pH was 5.4, with organic C 25.5 g kg⁻¹, total N 1.49 g kg⁻¹, available P 19.8 mg kg⁻¹, exchangeable K 108.0 mg kg⁻¹. The soil at Simao had pH 6.1, organic C 3.90 g kg⁻¹, total N 0.25 g kg⁻¹, available P 12.3 mg kg⁻¹, exchangeable K 108.0 mg kg⁻¹. At Na Pok, total N was not measured, but the pH was 5.8, organic C 1.30 g kg⁻¹, available P 15.7 mg kg⁻¹, and exchangeable K 12.0 mg kg⁻¹. Each site in China received 189, 108 and 121 kg ha⁻¹ of N, P and K respectively as a basal dressing, while 60, 30 and 30 kg ha⁻¹ of N, P and K was applied in Lao PDR. At Simao and Jing Hong, plot sizes of 2.0 m × 2.0 m were used, with a row spacing of 0.20 m, and with hills within the row spaced at 0.20 cm apart. Menglian used 1.2 m × 1.2 m plots with spacings of 0.15 and 0.15 m, while Na Pok used 1.5 m × 2.0 m plots, with 0.25 m rows and 0.15 m between hills within the row.

Table 2
Genotypes evaluated in perennial rice experiments at Simao, Menglian, Jing Hong and Na Pok in 2012 and 2013. Perennial rice entries were derived from the cross between *Oryza sativa* cv. RD23 and *O. longistaminata* (l.s.d. = 0.62; $P=0.05$).

Number	Genotype	Code	Yield (t ha ⁻¹)
1	2011.HN.FS.56	56	3.61
2	2011.HN.FS.59	59	3.31
3	2011.HN.FS.60	60	2.74
4	2011.HN.FS.75	75	1.94
5	2011.HN.FS.188	188	1.57
6	2011.HN.FS.214	214	3.56
7	2011.HN.FS.243	243	2.56
8	2011.HN.FS.246	246	2.74
9	2011.HN.FS.249	249	3.13
10	2011.HN.FS.251	251	2.77
11	2011.HN.FS.255	255	2.37
12	2011.HN.FS.264	264	2.99
13	2011.HN.Bt.69	Bt69	2.81
14	2011.HN.Bt.71	Bt71	2.82
15	2011.HN.147.5	147a	1.90
16	2011.HN.147.9	147b	1.73
17	2011.HN.139-12	139a	1.90
18	2011.HN.139-20	139b	1.62
19	2011.HN.137-12	137a	1.42
20	2011.HN.137-4	137b	1.30
21	Mutant TZ	TZ	2.25
22	PR23	PR23	4.25
	Mean		2.54

After puddling, each site was established by transplanting from adjacent seedbeds, with individual plants spaced 0.15 m apart in 0.25 m rows, and a plot size of 2.5 m × 1.5 m. After harvest, stubble was cut to 10 cm, so that consistent stubble for regrowth was available. Each site had access to irrigation, which was used to assist survival during the dry season, if needed. For each site, mean timings of transplanting and maturation, and successive cycles of stubble cut-off and maturation, were obtained, which defined growth duration in each cycle. Mean timings for each event were as follows, for dry season 2012, wet season 2012, dry season 2013, and wet season 2013, respectively: Jing Hong: 11 February to 21 May, 25 June to 28 October, 24 December to 12 June, and 1 August to 5 November. Menglian: 29 April to 12 August, 30 August to 7 January, 5 February to 9 July, 18 July to 22 October. Simao: 21 April to 23 August, and 25 February to 1 August (2012 and 2013 dry seasons); for the wet seasons at Simao, cut-off dates were 5 September 2012 and 1 September 2013, but no panicles were formed. At Na Pok, flush irrigation was applied in the dry season to keep plants alive, but no panicles were formed. Hence, at Na Pok, transplanting on 22 August 2012 meant its first crop was harvested at the end of wet season 2012, and a ratoon crop was harvested at the end of wet season 2013 only, but unfortunately, harvest dates were not recorded at Na Pok.

2.2. Germplasm and traits evaluated

The 22 genotypes (G) comprised *O. sativa* mutant TZ, and 21 perennial rice derivatives obtained from the cross between cultivated *O. sativa* cv. RD23 and the wild species *O. longistaminata* (Table 2). RD23 is a popular *indica* lowland rice cultivar released in Thailand, which is widely grown across south-east Asia, because of its broad adaptation, photoperiod insensitivity, high yield potential, good disease resistance and high grain quality (Chakhonkaen et al., 2012). In contrast, *O. longistaminata* is a wild rhizomatous perennial adapted to swampy regions, but with poor agronomic type (Hu et al., 2003). The cross between them was made with the intent of combining the perennial habit of *O. longistaminata*, with the agronomic features, broad adaptation and yield performance of RD23. Despite the interspecies cross, which required use of embryo rescue techniques, it proved possible to identify progeny able to

regrow after harvest, a few of which were also able to set seed. Further cycles of selection for fertility and agronomic type resulted in the materials tested here; specific details about the development of these breeding lines are reported by Zhang et al. (2014). The mutant TZ line, an off-type from line TZ, had been observed to ratoon strongly in breeding nurseries over cycles, so was included for comparison as an alternative perennial line. The 22 genotypes are referred to by their genotype code, e.g., 2011.HN.FS.56 is line 56 (Table 2).

Growth duration (days) was calculated from dates of transplanting and maturation, and successive cycles of stubble cut-off and maturation. Grain yield (t ha⁻¹), plant height (cm), rice ratooning rate (percent of plants with regrowth), ratoon tiller number (tillers per plant), and effective panicle number (fertile panicles per plant) were recorded from 0.9 m sections of the central four rows of each plot (24 plants or 0.9 m²). Ten panicle samples were used for panicle length (spikelets per panicle), grain number per panicle (grains per panicle), seed set rate (grains per spikelet), and grain size (weight of 1000 grains in g). Grain number per square metre (m⁻²) was calculated from grain yield and grain size.

2.3. Statistical analysis

Yield data for 22 genotypes and 12 environments were extracted from appropriate single-site analyses of variance (AOV). G×E interactions were analysed using the pattern analysis tool in Crop Stat (DeLacy et al., 1996). This method involved the joint application of cluster analysis and ordination to a transformed G×E matrix. Since the objective was to understand genotypic adaptation for breeding, the G×E matrix was transformed by environment standardisation (Cooper, 1999). The transformed data were clustered using an agglomerative hierarchical algorithm based on minimising incremental sum of squares (Ward, 1963). Scores for both genotypes and environments from the two-component interaction principal components model (IPCA) were computed for Axes 1, 2, 3 and 4, and plotted as biplots, with environment points at the end of spokes with labels as in Table 1, and genotype points as symbols with labels as in Table 2. Patterns of grain yield and other selected parameters were examined for genotype groups over environment groups, with means compared using l.s.d. with appropriate degrees of freedom for main effects and interactions, and associations among traits examined using Pearson correlations (Steel and Torrie, 1960).

3. Results

3.1. Environments

The range in temperatures at Na Pok was narrower than at the Chinese sites (Supplementary Table 1). In winter, minimum temperatures at Simao and Menglian dropped below 15 °C, while in summer, maximum temperatures at Jing Hong and Na Pok exceeded 35 °C. In the wet season, cut-off dates were later in Simao, exposing crops there to minimum temperatures as low as 6 °C, so no grain was harvested from wet season crops there. In contrast, rainfall effectively ceased in Na Pok in late September 2012 (Supplementary Table 2), and despite life-saving flush irrigation, growth was insufficient to allow grain formation in the 2013 dry season, as rainfall was well below average until April 2013. The soils at Menglian and Jing Hong were quite fertile, while those at Simao and Na Pok were lower in soil organic carbon (Table 3).

Site mean yield ranged from 0.94 t ha⁻¹ at Na Pok in the 2012 wet season to 6.04 t ha⁻¹ at Jing Hong in the 2012 dry season (Table 1). Yields were generally lower in the wet season than in the dry season, in the second year than in the first year, and thus tended to decline from growing season 1 to growing season 4. Genotype mean

Table 3
Cross site AOV for 2012 and 2013 G×E interaction studies with 22 genotypes in 12 environments.

Source	dF	SS	MS	F	%TSS	%G×E-SS
Environment	11	4,853,660	441,242	64.22**	47.3	
Genotype	21	1,426,702	67,938	9.89**	13.9	
G×E	231	2,170,891	9398	1.36**	21.1	
Residual	264	1,813,842	6871		17.7	
Total	527	10,265,095				
Stability regression	21	468,150	22,293			21.6
Regression deviations	210	1,702,741	8108			78.4
PCA component 1	31	104.364	3.367	15.73**		42.3
PCA component 2	29	47.036	1.622	7.58**		19.1
PCA component 3	27	40.754	1.509	7.05**		16.5
PCA component 4	25	22.441	0.89	4.16**		9.1
Residual	151	32.290	0.214			
Total	263	246.884				

yield (Table 2) ranged from 1.30 t ha⁻¹ in line 137b to 4.25 t ha⁻¹ in PR23, with mutant TZ intermediate (2.25 t ha⁻¹).

Environment main effects accounted for 57.4% of total sum of squares (T-SS), with genotype 16.9% and G×E interactions accounting for 25.7% (Table 3). Stability regression accounted for only 21.6% of G×E-SS. Cluster analysis on environment-standardised residuals identified 6 genotype groups × 7 environment groups, which preserved 74.4%, 91.4% and 55.6% of the E-SS, G-SS and G×E-SS, respectively. The ordination analysis of these residuals indicated four interaction principal component axes, accounting for 42.3%, 19.1%, 16.5% and 9.1% of the G×E-SS, respectively, or 87.0% in total (Table 3). Hence, two axes from ordination analysis preserved a similar proportion of interaction variability to the 6 G × 7 E grouping identified by cluster analysis.

The dendrogram for environments from cluster analysis (Fig. 1a) initially separated Menglian and Simao at higher altitudes in the north (Fusion 21) and Jing Hong and Na Pok at lower altitudes in the south (Fusion 22) (Fig. 1a). In the north, three Menglian environments (Fusion 18) separated from both dry season environments at Simao and the 2012 dry season environment at Menglian (Fusion 20). These Fusions (18 and 20) then split in turn, with Menglian 2013 Wet Season (Fusion 10–environment group E1) separating from Menglian 2012 Wet Season and Menglian 2013 Dry Season (Fusion 14–E2), and Simao 2013 Dry Season (Fusion 11–E3) separating from Simao 2012 Dry Season and Menglian 2012 Dry Season (Fusion 16–E4). In the south, the Na Pok environments (Fusion 17–E5) split from Jing Hong (Fusion 19), which in turn split into 2012 environments (Fusion 13–E6) and 2013 environments (Fusion 15–E7).

For the biplots from ordination analysis (Fig. 2a–c), all environments were negative for Axis 1, while Axis 2 separated the higher altitude environments in the north at Menglian and Simao which were positive (E1–E4), from the lower altitude environments in the south at Na Pok which were neutral to positive (E5), and at Jing Hong which were negative (E6 and especially E7) (Fig. 2a). Axis 3 (Fig. 2b) separated the positive Menglian 2013 Wet Season (E1) and Simao 2013 Dry Season (E3) environments from E2 and E4, respectively. Axis 3 also separated the negative Na Pok environments (E5) from the Jing Hong environments (E6 and E7). Axis 4 then separated the positive Menglian set (E1 and E2) from the negative Simao set (E3 and E4), with Jing Hong and Na Pok neutral (E5–E7) (Fig. 2c).

3.2. Genotypes and traits

In the dendrogram for genotypes from cluster analysis (Fig. 1b), a set of seven genotypes separated first (Fusion 37–genotype group G1), comprising lines 188, both 137s, both 139s and both 147s. Line TZ (Fusion 21–G2) separated next, then the remaining 14 lines (Fusion 41), separated into a larger group of 10 lines (Fusion 39),

and a smaller group of 4 lines (Fusion 40). Fusion 39 separated into two groups of five lines, comprising lines 60, 251, 264, Bt69 and Bt71 (Fusion 35–G3), and lines 75, 243, 246, 249 and 255 (Fusion 36–G4). In Fusion 40, PR23 (Fusion 22–G5) separated from lines 56, 59 and 214 (Fusion 38–G6).

In the biplots for genotypes from ordination analysis (Fig. 2a–c), biplot Axis 2 separated TZ (genotype group G2) which was negative, from all other entries, which were neutral (Fig. 2a). Axis 1 separated the positive G1 (lines 188, both 137s, both 139s and both 149s) from the negative G5 (PR23) and G6 (lines 214, 56 and 59), with the remaining ten lines neutral. Axis 3 then separated G5 (PR23) which was positive from G6 (lines 56, 59 and 214). Axis 3 also separated the positive G3 (lines 60, 251, 264, Bt69 and Bt71) from the neutral G4 (lines 75, 243, 246, 249 and 255). Axis 4 then aligned G3 with Simao (E3 and E4), G4 with Menglian (E1 and E2), G2 with Jing Hong 2013 (E7), G6 with Na Pok and Jing Hong 2012 (E5 and E6), while G1 was poorly adapted to all environments, and G5 was well adapted everywhere (Fig. 2c).

Grain yields are presented for 7 E × 6 G groups from cluster and ordination analysis (Table 4a). Among environment groups on average, the Jing Hong environments in 2012 (E6) were highest yielding (4.05 t ha⁻¹), followed by the pairs of northern environments (E2 and E4) which were intermediate (3.23 t ha⁻¹). The remaining environment groups were low yielding (1.59 t ha⁻¹), including Jing Hong 2013 (E7), Na Pok (E5), and the singleton Menglian 2013 Wet Season (E1) and Simao 2013 Dry Season (E3). Among genotype groups on average, PR23 (G5) was highest yielding (4.25 t ha⁻¹), followed by lines 56, 59 and 214 (G6), and these genotype groups were highest yielding in most environment groups. In contrast, G1 (lines 188, both 137s, both 139s and both 147s), which was lowest yielding at 1.54 t ha⁻¹, was also lowest yielding in most environment groups. While line TZ (G2) was also low yielding on average, it performed well in Jing Hong, especially in 2013 (E7) and was intermediate in Na Pok (E5), but failed at most northern sites. The remaining two groups were intermediate in yield, with G3 (lines 60, 251, 264, Bt69 and Bt71) performing well in Simao 2013 Dry Season (E3) but poorly in Na Pok (E5), while G4 (lines 75, 243, 246, 249 and 255) did poorly at both Simao 2013 Dry Season (E3) and Jing Hong 2013 (E7).

Growth duration (Table 4b) was quite variable across environments, ranging from an average of 96 days at Menglian 2013 Wet Season (E1) to 173 days at the 2 northern Dry Season sites (E4). Genotype TZ (G2) was considerably longer in duration (163 days) than the other lines, which averaged 136 to 149 days. The wide range in growth duration was mainly due to delayed maturity of genotype TZ in the Jing Hong environments (E6 and E7) and the 2 northern Menglian environments (E2). Without genotype TZ, the range in growth duration in each environment was only 4 to 15 days. But with TZ included, the range within environments was 8

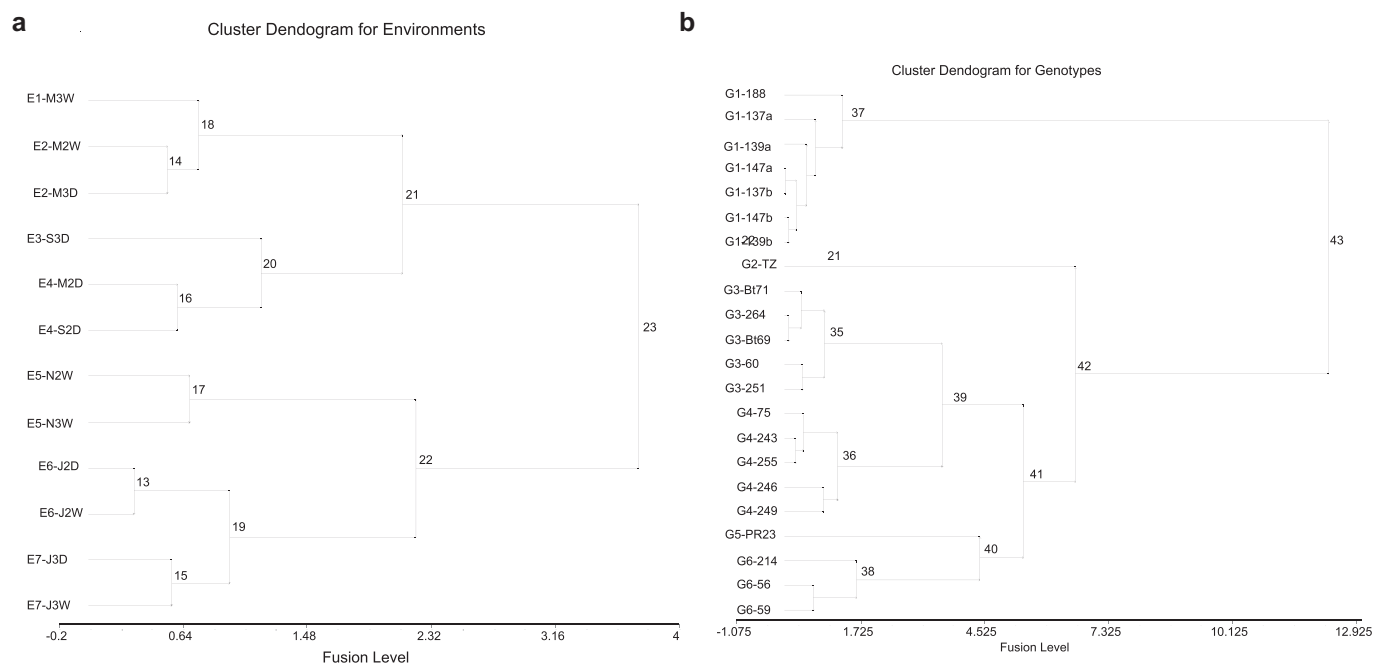


Fig. 1. (a) Environment groupings applied to standardised yield data for 22 perennial rice derivatives (*Oryza sativa* L., cv. RD23/*Oryza longistaminata*). The dendrogram shows fusion levels at which the groups join. The fusion level is proportional to the increase in within group SS at each fusion. The vertical dashed line represents the truncation of twelve environments into seven groups using Ward’s agglomerative clustering algorithm. Refer to Table 1 for environment abbreviations. (b) Genotype groupings applied to standardised yield data for 22 perennial rice derivatives (*Oryza sativa* L., cv. RD23/*Oryza longistaminata*) over 12 environments. The dendrogram shows fusion levels at which the groups join. The fusion level is proportional to the increase in within group SS at each fusion. The vertical dashed line represents the truncation of 22 genotypes into six groups using Ward’s agglomerative clustering algorithm. Refer to Table 2 for genotype abbreviations.

Table 4
Grain yield ($t\ ha^{-1}$), growth duration (d) and rice ratoon percentage (%) of 6 genotype groups across 7 environment groups (l.s.d. = 0.89 for grain yield, 1 for growth duration, and 12.2 for rice ratoon percentage, respectively; $P=0.05$).

Genotype Group	E1 (1) ^c	E2 (2)	Environment E3 (1)	Group E4 (2)	E5 (2)	E6 (2)	E7 (2)	Mean
<i>Yield (t ha⁻¹)</i>								
G1 (7) ^c	1.22	2.14	0.83	1.69	0.91	2.37	1.11	1.54
G2 (1)	0.0	2.08	0.0	0.0	2.02	5.35	4.03	2.25
G3 (5)	2.17	3.68	2.65	3.36	1.08	4.42	2.00	2.82
G4 (5)	1.81	4.38	0.40	2.98	1.50	4.05	1.26	2.55
G5 (1)	4.91	6.29	2.88	3.63	1.67	6.56	3.43	4.25
G6 (3)	1.40	4.02	1.96	4.22	3.00	6.09	1.95	3.49
Mean	1.79	3.61	1.42	2.85	1.45	4.05	1.70	2.54
<i>Duration (d)</i>								
G1 (7)	98	144	158	171	M ^a	126	135	141
G2 (1)	95	145	158	204	M	161	179	163
G3 (5)	92	146	164	172	M	128	129	140
G4 (5)	92	139	153	170	M	124	125	136
G5 (1)	107	143	159	164	M	127	137	141
G6 (3)	103	138	152	179	M	128	137	149
Mean	96	143	157	173	M	128	133	141
<i>Ratoon (%)</i>								
G1 (7)	41.6	60.5	50.1	n.a. ^b	M	96.5	57.8	60.6
G2 (1)	81.7	83.4	44.6	n.a.	M	100.0	83.8	79.9
G3 (5)	42.7	73.4	66.2	n.a.	M	97.1	80.2	73.3
G4 (5)	25.8	74.5	20.8	n.a.	M	98.5	34.6	51.9
G5 (1)	70.0	86.9	64.2	n.a.	M	100.0	79.0	80.8
G6 (3)	13.5	71.4	30.3	n.a.	M	97.6	45.8	53.7
Mean	37.5	70.4	44.8	n.a.	M	97.6	58.1	62.4

^a M = missing.

^b n.a. = not applicable, as rice ratoon percentage can only be recorded from regrowth.

^c Numbers of group members in parentheses.

to 54 days, with the greatest delay (to 179 days) at the Jing Hong 2013 sites (E7).

Rice ratoon percentage (Table 4c) could only be recorded from ratoon crops, not the first crop at each site, i.e., the 2 northern Dry Season sites in 2012 (E4), Jing Hong 2012 Dry Season (in E6), and Na Pok 2012 Wet Season (in E5). Hence, ratoon percentage was not

applicable in E4, and the only missing values were for Na Pok 2013 Wet Season (in E5), where this trait was not recorded. Among environments, rice ratoon percentage ranged from 97.6% at Jing Hong 2012 (E6) to 44.8% at Simao 2013 Dry Season (E3) and 37.5% at Menglian 2013 Wet Season (E1). For genotypes, rice ratoon percentage ranged from 80.0% in G2 and G5, to 53.0% in G4 and G6. TZ

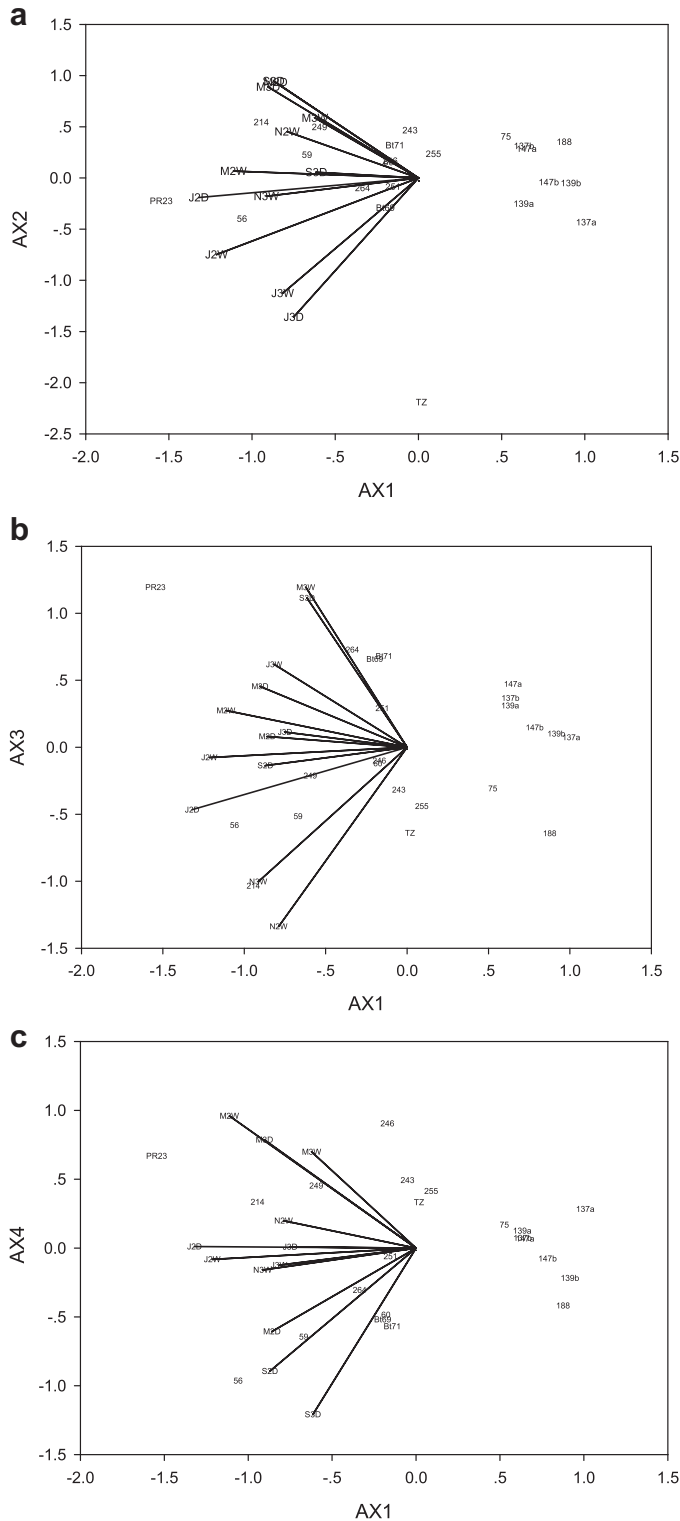


Fig. 2. (a) Principal component analysis (location standardised) for the environment \times genotype interaction for Axis 1 and Axis 2 for grain yield for 12 environments and 22 perennial rice derivatives (*Oryza sativa* L., cv. RD23/*Oryza longistaminata*). Refer to Tables 1 and 2 for genotype and environment abbreviations. The G \times E interaction for Axis 1 and Axis 2 accounted for 61.4% of the sum of squares. (b) Principal component analysis (location standardised) for the environment \times genotype interaction for Axis 1 and Axis 3 for grain yield for 12 environments and 22 perennial rice derivatives (*Oryza sativa* L., cv. RD23/*Oryza longistaminata*). Refer to Tables 1 and 2 for genotype and environment abbreviations. The G \times E interaction for Axis 1 and Axis 3 accounted for 58.8% of the sum of squares. (c) Principal component analysis (location standardised) for the environment \times genotype interaction for Axis 1 and Axis 4 for grain yield for 12 environments and 22 perennial rice derivatives (*Oryza sativa* L., cv. RD23/*Oryza longistaminata*). Refer to Tables 1 and 2 for genotype and environment abbreviations. The G \times E interaction for Axis 1 and Axis 4 accounted for 51.4% of the sum of squares.

(G2) had the highest ratoon percentage, except in Simao 2013 Dry Season (E3), where only G3 and G5 exceeded 60.0%. G4 and G6 generally had the lowest ratoon percentages, with G1 lowest at the 2 northern Menglian sites (E2). PR23 (G5) generally had high ratoon percentages in every environment group.

3.3. Trait associations

The main effects of environment group and genotype group on trait expression are shown in Table 5. Among environments, Jing Hong 2012 (E6) was highest yielding, and was also highest in grain number m^{-2} , seed setting rate, panicle length, grains per panicle, plant height and rice ratoon percentage. The 2 Menglian Dry Season environments (E4) were also high yielding, and were high in grains m^{-2} , rice ratoon percentage and ratoon tiller number. The Jing Hong 2013 environments (E7) were high in ratoon tiller number but low in grain number m^{-2} . Na Pok (E5) also had low grain number m^{-2} and the smallest grain size. Simao 2013 Dry Season (E3) was long in growth duration and highest in ratoon tiller number and effective panicle number, while the 2 northern Dry Season sites (E4) had the longest growth duration and the largest grain size. Menglian 2013 Wet Season (E1) was low yielding, shortest in growth duration, had the lowest ratoon percentage, ratoon tiller number and effective panicle number. Among genotypes (Table 5), PR23 (G5) was highest in grain yield, and also in rice ratoon percentage, ratoon tiller number, effective panicle number, grain number m^{-2} , seed set rate and grain size. G6 (lines 56, 59, 214) was next highest yielding, and also had high values for these parameters. In contrast, G1 was low yielding, and had generally low values except for ratoon tiller number. Line TZ (G2) was tall and late, with lower grain number m^{-2} . G3 and G4 were intermediate in yield and most parameters, but had the largest grain number per panicle.

These trait associations can be summarised using a Pearson correlation analysis. Among environments, grain yield was correlated with grain number m^{-2} ($r=0.99^{**}$), ratoon percentage with grain number m^{-2} ($r=0.45^*$) and grain yield ($r=0.46^*$), seed set rate with grain size ($r=0.42^*$) and grain yield ($r=0.41^*$), ratoon tiller number with growth duration ($r=0.58^*$) and effective panicle number ($r=0.59^*$), and grain size was inversely correlated with grain number per panicle ($r=-0.66^*$). For genotypes, grain yield was correlated with grain number m^{-2} ($r=0.98^{**}$), seed set rate with grain size ($r=0.47^*$) and both grains m^{-2} ($r=0.85^{**}$) and grain yield ($r=0.88^{**}$), ratoon percentage with ratoon tiller number ($r=0.73^{**}$), and grain size was inversely correlated with grains per panicle ($r=-0.49^*$).

4. Discussion

In this study, G \times E interaction accounted for 25.7% of the total sum of squares for grain yield, which, together with Genotype, accounted for 42.6% of the total variation. Four vectors accounted for 87.0% of G \times E, suggesting a high repeatable component, which was consistent with other studies in rice (Botwright Acuna et al., 2008). The consistent grouping of sister lines (e.g., lines 137a and 137b) within the same genotype group (Fig. 2) also indicated a strong component of repeatable interaction, which was also consistent with other studies (Wade et al., 1999). Consequently, cluster and ordination analysis reduced the matrix from 22 individual genotypes \times 12 individual environments (=264) to 6 genotype groups \times 7 environment groups (=42), whilst retaining the repeatable variation for interpretation.

4.1. Environment groupings

The 12 environments were grouped by cluster and ordination analysis into distinct groups that could be defined by the condi-

Table 5
Main effect of environment and genotype groupings on yield components of perennial rice derivatives: growth duration (Duration), plant height (Height), plant ratoon percentage (PRP), ratoon tiller number (RTN), effective panicle number (EPN), panicle length (PL), grain number per plant (GN), grain number per spikelet (GPS), 1000 grain weight (GWT), grain number per unit area (GNO), and grain yield (Yield) (l.s.d. are shown for $P=0.05$).

	Duration (d)	Height (cm)	RRP (%)	RTN (pl ⁻¹)	EPN (pl ⁻¹)	PL (panicle ⁻¹)	GN (panicle ⁻¹)	GPS (spikelet ⁻¹)	GWT (g 1000 ⁻¹)	GNO (10 ³ m ⁻²)	Yield (t ha ⁻¹)
<i>Environment group</i>											
E1 (1) ^a	96	82	39	9.6	3.9	22.3	121	0.67	23.6	7.6	1.79
E2 (2)	143	80	70	13.0	6.8	19.3	82	0.67	23.8	15.2	3.61
E3 (1)	157	102	47	15.4	21.1	23.1	121	0.68	23.3	6.1	1.42
E4 (2)	173	109	63	13.0	8.9	22.4	135	0.60	24.0	11.9	2.85
E5 (2)	n.a.	n.a.	n.a.	n.a.	n.a.	21.7	n.a.	n.a.	20.1	7.2	1.45
E6 (2)	128	107	80	12.8	11.7	23.9	146	0.72	23.6	17.4	4.05
E7 (2)	133	99	58	13.9	11.3	22.6	124	0.66	23.3	7.3	1.70
Mean	138	96	60	12.9	10.6	22.2	121	0.67	23.1	10.4	2.54
<i>l.s.d.</i>	3	2.3	6	1.3	0.9	0.5	9	0.02	0.5	0.9	0.34
<i>Genotype group</i>											
G1 (7) ^a	140	100	62	14.0	10.2	22.2	118	0.6	23.4	8.2	1.91
G2 (1)	163	122	77	13.6	9.8	23.2	117	0.73	25.0	9.0	2.25
G3 (5)	141	99	70	13.0	9.8	22.7	124	0.70	22.6	14.2	3.18
G4 (5)	136	92	56	11.7	10.3	22.0	125	0.7	23.7	11.6	2.76
G5 (1)	141	96	75	14.7	10.8	19.6	111	0.78	25.5	16.6	4.25
G6 (3)	142	87	56	12.1	10.9	22.0	122	0.75	24.7	14.6	3.59
Mean	144	100	66	13.2	10.3	21.9	120	0.7	24.2	12.4	2.54
<i>l.s.d.</i>	10	10.6	12	3	2.9	1.81	22	0.11	1.7	3.7	0.62

^a Numbers of group members in parentheses.

tions encountered, and the way they influenced genotype response. At higher altitude in the north, the environments in Simao were defined by minimum temperature (Supplementary Table 1). In the Wet Season, crops failed to produce grain, due to low temperature slowing growth and delaying flowering. In the 2013 Dry Season, ratoon percentage was restricted by low minimum temperature in combination with rainfall deficit during February–April, with grain number m⁻² also limited by low minimum temperature during panicle elongation and flowering during May–June (Supplementary Table 1). At Menglian, the 2013 Wet Season crop encountered heavy rainfall in August which may have affected ratoon percentage. It also encountered low temperature around flowering in October–November (Supplementary Table 1), restricting its grain number m⁻². At lower altitudes in the south, minimum temperature was less of a problem, but periods of rainfall deficit in combination with high evaporative demand and high temperature could become limiting (Supplementary Table 2). The Jing Hong 2013 Dry Season crop encountered high evaporative demand together with rainfall deficit up to flowering through January–April (Supplementary Table 2), which restricted its grain number m⁻². Na Pok 2012 Wet Season encountered a severely dry finish in September–December (Supplementary Table 2), which restricted its grain size. Lack of rainfall precluded dry season crop yield at Na Pok, though plants survived the dry season with the benefit of life-saving flush irrigation. These environmental factors defined the environment groupings, and the basis of genotype group response, as discussed in Section 4.2.

In the dendrograms (Fig. 1a), environment groups were initially separated by mean temperature, with the cooler environments in Menglian and Simao at higher altitudes in the north separating from the lower altitude and warmer environments in Na Pok and Jing Hong in the south. Seasonal conditions provided the next separation. In the north, mainly Dry Season environments at Simao separated from mainly Wet Season environments at Menglian. Minimum temperatures then separated Simao 2013 Dry Season and Menglian 2013 Wet season from their respective Simao and Menglian groups. In the south, environments at Na Pok separated from environments at Jing Hong, with Jing Hong in turn separating by year. This separation of environments in the south was mainly due to high evaporative demand in conjunction with rainfall deficit (Supplementary Table 2), especially for Jing Hong 2012 Dry Season and Na Pok 2013 Wet Season.

For the biplots (Fig. 2a), Axis 1 was interpreted to represent yield potential, which was clearly shown by the genotype groupings discussed below in 4.2. The genotype groupings in 4.2 also clearly demonstrated Axis 2 represented delay in phenology, which was affected by the environmental stresses discussed above, and delay was most severe in Jing Hong in 2013. Axis 3 (Fig. 2b) represented rice ratoon percentage, with low values in Simao 2013 Dry Season and Menglian 2013 Wet Season in particular. Finally, Axis 4 (Fig. 2c) separated Menglian (positive), from Simao (negative), with Jing Hong and Na Pok neutral, and clearly revealed patterns of genotype group adaptation, as discussed below.

4.2. Adaptation of genotype groups to low temperature and rainfall deficit

The 22 Genotypes were grouped by cluster and ordination analysis by their responses to the environmental challenges above. This is best illustrated in the biplots (Fig. 2a–c), with Axis 1 separating high-yielding groups G5 (PR23) and G6 (lines 56, 59 and 214) to the left, intermediate-yielding groups G3 (lines 60, 251, 264, Bt69, Bt71) and G4 (lines 75, 243, 246, 249, 255) to the middle, and low-yielding group G1 (lines 188, both 137s, both 139s, both 147s) to the right. Axis 2 separated the remaining group G2 (line TZ), whose phenology was strongly delayed under environmental stress, from the other groups. Axis 3 separated genotype groups by ratoon percentage, with strong regrowth in G5 (PR23) at the top. Axis 4 summarised the patterns of genotype adaptation across the environment groups, based on the projection of each genotype or genotype group on the respective environment vectors (Yan, 2002; Botwright Acuna and Wade, 2013). Thus, G5 (PR23) was widely adapted to all environments, G4 (lines 75, 243, 246, 249, 255) preferentially adapted to Menglian environments, G3 (lines 60, 251, 264, Bt69, Bt71) preferentially adapted to Simao environments, G2 (TZ) to Jing Hong 2013, G6 (lines 56, 59, 214) to Jing Hong 2012 and Na Pok environments, while G1 (lines 188, both 137s, both 139s, both 147s) was poorly adapted everywhere (Fig. 2c).

These relationships imply genotypic differences in trait expression among the genotype groups, not only in the measured parameters presented, but also for traits implicated in providing adaptive advantage across the range of environments sampled. For example, the preferential adaptation of G3 (lines 60, 251, 264, Bt69, Bt71) to Simao implies these lines may possess some escape of

or tolerance to low temperature conditions, in ratooning ability, spikelet fertility, or both. Likewise, G4 (lines 75, 243, 246, 249, 255) may possess some preferential adaptation to wet season conditions, since that dominated the Menglian response. In contrast, G6 (lines 56, 59, 214) may possess traits of benefit in the south, where higher temperatures and rainfall deficit were more important. It would be worth screening for these traits, as discussed below.

The high yield and broad adaptation shown by PR23 makes it a compelling candidate for release to farmers, and it is already under pre-release field testing in small plots, as well as field-scale evaluation with a commercial company. With access to supplementary irrigation in the dry season, these results confirm PR23 can survive, regrow and produce grain over four successive seasons from a single planting at a number of locations. This is an important finding, since, in a companion study in southern Lao PDR, Samson et al. (2016) reported that the annual rice cultivar RD23 failed to survive the dry season, despite access to life-saving flush irrigation, and had to be replanted. In contrast, of the 12 perennial rice derivatives they tested, all survived, regrew and contributed grain, with the best lines yielding comparably to RD23 from regrowth in the following wet season. Nevertheless, further testing is needed to determine the extent of this longevity in perennial rice, and whether performance can be retained in subsequent cycles of regrowth.

4.3. Implications for breeding of perennial (and annual) rices

Relative to studies of genetically-diverse rice cultivars under upland (Lafitte and Courtois, 2002; Atlin et al., 2006) and rainfed-lowland (Cooper et al., 1999; Wade et al., 1999) environments, where G×E was large relative to G, the ratio here was only 1.5. While this could be taken to suggest G×E is lower in perennial than annual rice, care should be taken in drawing this conclusion. The preliminary lines evaluated here are all effectively selected from a single cross between one *O. sativa* cultivar (RD23), and one *O. longistaminata* accession (Zhang et al., 2014). The advantage of these materials is the combination of capacity for post-sexual cycle regrowth and retention of spikelet fertility, which is not readily attained. In order to broaden the genetic base, however, effort is now being made to backcross these traits into a range of annual rice cultivars of diverse origin and adaptation. Not only would this allow these perennial traits to be tested in different backgrounds, but intercrossing the progeny would facilitate the development of and selection in segregating populations, in a manner analogous to the model proposed by Larkin et al. (2014) for perennial wheat.

The patterns of adaptation revealed in this paper suggest perennial rice lines should be selected for adaptation to low temperature, especially during early regrowth for effective ratoon tiller number, and around panicle elongation and flowering for spikelet fertility. Selection procedures for adaptation to low temperature based on those developed in Australia (Farrell et al., 2006; Ye et al., 2009) should prove beneficial, in developing improved annual or perennial rices for more northern locations such as Menglian and Simao. Conversely, adaptation to rainfall deficit would be beneficial in more southern locations such as Jing Hong and Na Pok. Selection procedures developed in Thailand, Laos and Cambodia (Fukai et al., 1999; Xangsayasane et al., 2014) for improving drought tolerance of rainfed rice should also be beneficial here, for both annual and perennial rice. The intent should be to retain yield potential while also improving survival, regrowth and performance under drought (Atlin et al., 2006; Venuprasad et al., 2008; Blum, 2009, 2011).

5. Conclusions

Current lines of perennial rice were able to survive, regrow and produce grain for up to four successive growing seasons at

a number of locations, especially when supplementary irrigation was available to assist survival during the dry season. The results demonstrated that PR23 was high-yielding and broadly-adapted, making it a prime candidate for release to farmers. Besides being in pre-release testing in Yunnan Province of China, PR23 is also under commercial evaluation there in lowland fields under irrigation, with mechanical transplanting and harvesting, and an expectation of cost-savings relative to annual rice. Indeed, the promising results here suggest that, with further selection, high-yielding perennial rices could even have a place alongside high-yielding annual rices in favourable and irrigated environments in the future. Nevertheless, many perennial rice lines survived environmental stresses in the field, including rainfall deficit, implying a capacity to perform without supplementary irrigation where dry seasons are mild or short, but this remains to be properly tested, as does the extent of longevity beyond four successive seasons in the field. The ways in which farmers may utilise the availability of perennial rice for their farming system remains to be examined, given in many situations, livestock are part of the system, so perennial rice could contribute fodder for grazing as well as grain, while retaining ground cover and viable root systems. The ecosystem benefits of perennial rice for soil and nutrient retention remain to be tested. Socio-economic impact should also be assessed, as should farmer perception of perennial rice. Finally, any trade-off in yield potential due to perennial habit needs to be quantified, in relation to resource capture and allocation in the plant.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fcr.2017.03.007>.

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多年生稻稻瘟病抗性评价

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摘要:利用长雄野生稻(*Oryza longistaminata*)地下茎无性繁殖特性培育多年生稻(Perennial Rice, PR)已经成功并开始示范推广。多年生稻表现出一定的稻瘟病抗性,但其所具有的稻瘟病抗性来源尚不清楚。本研究通过田间病情调查、接种鉴定以及抗性基因检测等3种方法,对育成的多年生稻23(PR23)、云大24(PR24)、云大25(PR25)、云大101(PR101)、云大107(PR107)、父本长雄野生稻、母本RD23、(RD23/长雄野生稻) F_1 进行稻瘟病抗性评价。结果表明,父本长雄野生稻、(RD23/长雄野生稻) F_1 代及5个多年生稻品种(系)表现为高抗稻瘟病,而母本RD23表现高感稻瘟病,推测PR23、PR24、PR25、PR101和PR107这5个多年生稻品种(系)的稻瘟病抗性可能来源于长雄野生稻。其中,PR23、PR25稻瘟病抗性基因可能来自于长雄野生稻的*Pi5*基因和*Pita-2*位点,PR24稻瘟病抗性基因可能是来自长雄野生稻的*Pita-2*位点,PR107稻瘟病抗性基因可能来自于长雄野生稻的*Pi5*基因和*Pish*位点;PR101中未检测到本文中涉及到的基因或位点,推测其稻瘟病抗性来自长雄野生稻内未知的稻瘟病抗性基因。本研究结果将为多年生稻稻瘟病抗病育种、品种布局、植保技术制定等提供一定参考。

关键词:多年生稻;稻瘟病;抗性评价;长雄野生稻

中图分类号:S435.111.4*1;S511 **文献标识码:**A **文章编号:**1006-8082(2021)01-0009-05

稻瘟病是由稻梨孢菌(*Magnaporthe oryzae*)引起的水稻真菌病害之一,具有发病急、破坏力强、发病地区广泛、发病时期及发病部位类型多、造成经济损失严重等病害特征^[1]。利用抗病基因改良品种是目前防治该病害最有效的措施,至今已定位了100多个稻瘟病抗性主效基因,并克隆了30多个稻瘟病抗性主效基因^[2]。利用已开发的功能分子标记,可准确地检测不同水稻品种中存在的稻瘟病抗性基因^[3]。

利用长雄野生稻地下茎无性繁殖特性培育的多年生稻已在生产上推广应用^[4-6]。多年生稻不仅能实现免耕、减缓耕作带来的水土流失等问题,同时还能减少人力和农资投入^[7]。在多年生稻试验示范和推广过程中发现,其对稻瘟病具有一定抗性,但具体的抗性水平和抗病基因还未明晰。虽然已发现长雄野生稻第12号染色体上具有一定稻瘟病广谱抗性基因*Pi57*^[8],但该基因是否导入多年生稻品种(系)并引起相应抗性反应还未可知。因此,本研究对5个多年生稻品种(系)PR23、PR24、PR25、PR101、PR107,及其父本长雄野生稻、母本RD23及(RD23/*O. longistaminata*) F_1 进行田间病情调查、接种抗性鉴定,以及分析已知的多个R基因在多年生稻品种(系)中有无,初步明确多年生稻对稻瘟病的抗性情况,为多年生稻的稻瘟病抗病育种和生产布局提供参考。

1 材料与方法

1.1 试验材料

以多年生稻品种(系)PR23、PR24、PR25、PR101、PR107、长雄野生稻(多年生稻父本)、泰国优质籼稻RD23(多年生稻母本)、(RD23/*O. longistaminata*) F_1 及本地感稻瘟病品种丽江新团黑谷(LTH)为供试品种。

供试稻瘟病菌为强致病力CH091C菌株,由云南省农业科学院农业环境资源研究所保存和提供。

1.2 田间病情调查

2019年6月,在云南省西双版纳州多年生稻示范推广田块进行多年生稻品种(系)的叶瘟田间病情情况调查。采用五点取样法,各品种(系)取样数量为100株,参照国际水稻研究所叶瘟抗性评价分级标准^[9]进行病级分级,按照病情指数= \sum (各级病株数×该病级值)/(调查总株数×最高级值)×100进行病情指数计算。病情指数为0表示高抗(HR),0~5%表示抗(R),5.1%~15%表示中抗(MR),15.1%~25%为中感(MS),25.1%~50%为感(S),>50%为高感(HS)。水稻苗瘟、叶瘟抗性

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表 1 水稻苗瘟叶瘟抗性分级标准(IRRI)

病级	受害情况	抗性水平
0	叶片无病斑	高抗(HR)
1	病斑为针头大小褐点	抗(R)
2	褐点稍大	抗(R)
3	圆形至椭圆形的灰色病斑, 边缘褐色, 病斑直径 1~2 mm	中抗(MR)
4	梭形病斑, 长 1~2 cm, 通常局限于两条叶脉间, 受害面积不超过叶面积的 2%	中抗(MR)
5	梭形病斑, 受害面积不超过叶面积的 10%	中感(MS)
6	梭形病斑, 受害面积不超过叶面积的 11%~25%	中感(MS)
7	梭形病斑, 受害面积不超过叶面积的 26%~50%	感(S)
8	梭形病斑, 受害面积不超过叶面积的 51%~75%	感(S)
9	全叶枯死	高感(HS)

表 2 稻瘟病抗性基因检测的引物序列及相关信息

目的基因	前引物序列	后引物序列	目标片段/bp		退火温度 /°C	文献
			抗病(R)	感病(S)		
<i>Piz1</i>	ATGTGGATGCTGTGTAT	TAGTTTGCTGCTCAATAAGTA	176		55	[10]
<i>Pi2</i>	CAGCGATGGTATGACACAA	CGTTCCTATACTGCCACATCG	450	282	53	[11]
<i>Pi9</i>	GCTGTGCTCCAAATGAGGAT	GCGATCTCACATCCTTTGCT	291		55	
<i>Pikh</i>	CCCAACATTTGGTAGTAGTC	TCCTTCATACGCAACAATCT	258	401	51	[12]
<i>Pi5</i>	ATAGATCATGCGCCCTCTTG	TCATACCCCATTCGGTTCATT	206	307	57	[11]
<i>Pik</i>	GGATAGCAGAAGAACTTGAGACTA	CATGTCITTTCAACATAAGAAGTTCTC	140		55	
	GGATAGCAGAAGAACTTGAGACTG	CATGTCITTTCAACATAAGAAGTTCTC		140		
<i>Pikp</i>	GGTGTTTGGGAACCTGAACCCT	TTTCTGTTCGTCGGATGCTC	158		55	
	GGTGTTTGGGAACCTGAACCCTG	TTTCTGTTCGTCGGATGCTC		158		
<i>Pi1</i>	GTGCTGCTGTGGCTAGTTTG	AGTCCCCGCTCAATTTTTCT	460		58	[13]
<i>Pikm-1</i>	CAGTAGCTGTCTCAGAACTATG	AAGGTACCTCTTTTGGGCCAG	290	323	56	[14]
<i>Pikm-2</i>	TGAGCTCAAGGCAAGAGTTGAGGA	TGTTCAGCAACTCGATGAG	174	213	58	[14]
* <i>Pita-2</i>	TTGAGAGCCTTTTAGGATG	TGGTTTACTTGGTTACTCG	169		55	
<i>Piz</i>	GCATTTTTAGCTATGAATCTGGAT	TGTAGAATGAGGTGAGTTATTAACA	200		55	
* <i>Pish</i>	CCACTTTCAGCTACTACCAG	CCACTTTCAGCTACTACCAG	136		55	[15]
* <i>Pi7</i>	CCACTTTCAGCTACTACCAG	GAGCCTTCTGGTTTCTGCTATGC	184		55	[15]
* <i>Pi20</i>	GAGATGGCCCCCTCCGTGATGG	TGCCCTCAATCGGCCACACCTC	255		55	[16]
* <i>Pi57</i>	GTATTACGCTCGATACGGCC	GTATCCTTTCTCGCAATCGC	148		55	[8]
	GTATTACGCTCGATACGGCC	GTATCCTTTCTCGCAATCGC	169		55	

* 为 SSR 连锁分子标记。

分级标准见表 1。

1.3 苗瘟抗性水平评价

以 LTH 为感病对照, 利用 5% 次氯酸钠对 RD23、PR23、PR24、PR25、PR101、PR107 种子以及长雄野生稻地下茎尖组织进行消毒后催芽, 每个材料在播种盘(规格为 30 cm×10 cm)中播 2 行, 每行 10 株, 共 20 株, 待长至 3 叶 1 心时接种稻瘟病菌。稻瘟病菌 CH091C 菌株于燕麦培养基(燕麦 10.0 g、琼脂 4.0 g、蔗糖 5.0 g, 加水至 300 mL, 120°C 高温高压灭菌)上进行活化培养, 培养 7 d 后将菌丝洗净放置于光照培养箱中, 产孢培养 2 d 后配置浓度约 1×10^5 个/mL 孢子悬浮液。用喷壶均匀喷洒于水稻叶片上, 放置于培养箱中 25°C 保湿培养 24 h。接种 7 d 后, 参照国际水稻研究所苗瘟抗性

鉴定分级标准进行抗性水平鉴定。

1.4 稻瘟病抗性基因检测

利用已知的多个稻瘟病抗性基因功能标记和紧密连锁 SSR 标记对多年生稻材料进行 PCR 扩增(表 2), 扩增产物利用 1.0% (目标产物 >500bp) 或 2.0% 的琼脂糖凝胶和 8% 聚丙烯酰胺凝胶电泳进行检测(目标产物 <500 bp)。

2 结果与分析

2.1 稻瘟病田间病情调查结果

通过调查多年生稻示范推广田的稻瘟病发病情况, 发现多年生稻品种(系)和父本长雄野生稻无明显叶瘟症状, 呈现较强的稻瘟病抗性, PR23、PR24、PR25、

表 3 多年生稻品系(种)田间病情调查和苗瘟抗性评价结果

材料名称	田间叶瘟病级	田间病情指数/%	田间叶瘟抗性评价	苗瘟抗性水平评价
长雄野生稻	0 级	0	HR	R
RD23	3~8 级	63.33	HS	S
F ₁	0~1 级	0.74	R	-
PR23	0~1 级	1.44	R	R
PR24	0~2 级	1.47	R	R
PR25	0~2 级	1.56	R	R
PR101	0~1 级	1.11	R	R
PR107	0~2 级	1.33	R	R
LTH	-	-	-	S

表 4 10 个 R 基因在多年生稻品系(种)及亲本中的分布检测

R 基因	长野	RD23	F ₁	PR23	PR24	PR25	PR101	PR107	Yes/No	单基因系	CH091C 鉴定反应
<i>Pik</i>	+	-	-	-	-	-	-	-	N	KRBLK KA	R
<i>Pikp</i>	-	-	-	-	-	-	-	-	N	KRBLKP-K60	R
<i>Pi5</i>	+	-	-	+	-	+	-	+	Y	IRBL5-M	R
<i>Pi2</i>	-	-	-	-	-	-	-	-	N	IRBLZ5-CA	R
<i>Pizt</i>	+	+	+	+	+	+	+	+	N	IRBLZT-T	R
<i>Pi1</i>	-	+	+	+	+	+	-	-	N	IRBL1-CL	R
<i>Pi54</i>	+	+	+	-	+	-	+	-	N	KRBLKH-K3	R
<i>Pi9</i>	+	+	+	-	-	-	+	-	N	IRBL9-W	R
<i>Pikm</i>	+	-	-	-	-	-	-	-	N	IRBLKM-TS	R
<i>Piz</i>	-	+	+	+	+	+	+	+	N	IRBLZ FU	R

“+”携带 R 基因;“-”不携带 R 基因。

表 5 5 个 R 基因在多年生稻及其亲本中的多态性检测

R 基因	长野	RD23	F ₁	PR23	PR24	PR25	PR101	PR107	Yes/No	单基因系	CH091C 鉴定反应
<i>Pish</i>	R	S	H	S	S	S	S	R	Y	IRBLSH-S	R
<i>Pi7</i>	S	R	H	S	S	S	S	S	N	IRBL7-M	R
<i>Pita-2</i>	R	S	H	R	R	R	S	S	Y	IRBLTA2-PI	R
<i>Pi20</i>	S	S	S	S	S	S	S	S	N	IRBL20-IR24	R
<i>Pi57</i>	R	S	S	S	S	S	S	S	N	-	R

R, 扩增目的条带; S, 扩增非目的条带; H, 扩增分别来自 2 个亲本的目的带和非目的带。

PR101、PR107、长雄野生稻、F₁ 病情指数分别为 1.44%、1.67%、1.56%、1.11%、1.33%、0、0.74%(表 3)。而母本 RD23 具有典型稻瘟病斑, 调查病株最轻病级达 3 级(叶片出现椭圆灰白病斑), 大部分病株病级分布于 5~7 级(受害面积 10%~50%), 最高病级可达 8 级(叶部受害面积为 51%~75%), 病情指数为 63.33%(表 3)。

2.2 苗瘟抗性水平评价

接种强致病力稻瘟病菌 CH091C 菌株 7 d 后, PR23、PR24、PR25、PR101、PR107 和长雄野生稻仅有针尖大小病斑, 表现为抗病。而感病对照丽江新团黑谷(LTH)和多年生稻品种(系)母本 RD23 均具有典型叶瘟症状, 表现为感病(表 3)。多年生稻品种(系)苗期接种稻瘟病菌进行稻瘟病抗性水平鉴定与田间病情调查结果较为一致, 说明多年生稻品系(种)具有较强的抗瘟性, 同时该特性可能来源于父本长雄野生稻。

2.3 稻瘟病抗性基因检测

利用功能标记检测 10 个已知的 R 基因在多年生稻中的分布, 在 PR23 和 PR25 中均检测到抗性基因 *Pizt*、*Pi5*、*Pi1*、*Piz*, 但只有 *Pi5* 在长雄野生稻以及 PR23、PR25 中检测得到, 且在 RD23 中缺失, 所以 PR23、PR25 所携带的 *Pi5* 基因可能来源于长雄野生稻(表 4)。

PR107 携带 *Pizt*、*Piz*、*Pi5* 稻瘟病抗病基因, 仅 *Pi5* 在长雄野生稻检测到, 而 RD23 中缺失, 因此来源于长雄野生稻的 *Pi5* 可能为 PR107 的稻瘟病抗病基因(表 5)。

利用与 *Pish*、*Pita-2*、*Pi7*、*Pi20*、*Pi57(t)* 基因分别连锁的 SSR 标记 RM212(*Pish*)、RM6905(*Pita-2*)、RM27384/RM27386(*Pi7*)、OSR32(*Pi20*)、RM5364/RM7102(*Pi57(t)*) 对 5 个多年生稻品系(种)进行基因型评价, 发

现 PR23、PR24、PR25 中携带来自长雄野生稻的 *Pita-2* 位点, 而 PR107 中携带来自长雄野生稻的 *Pish* 位点 (表 5)。推测 PR23、PR24、PR25 的稻瘟病抗性基因可能来源于长雄野生稻的 *Pita-2* 位点, 而 PR107 的稻瘟病抗性基因可能来源于长雄野生稻的 *Pish* 位点。

因此, PR23 和 PR25 的稻瘟病抗性基因可能来源于长雄野生稻的 *Pi5* 基因和 *Pita-2* 位点, PR24 稻瘟病抗性基因可能来源于长雄野生稻的 *Pita-2* 位点, PR107 稻瘟病抗性基因可能来源于长雄野生稻的 *Pi5* 基因和 *Pish* 位点, 本文涉及到的稻瘟病抗性基因或位点 PR101 中均不存在, 推测其稻瘟病抗性来自长雄野生稻未知的稻瘟病抗性基因。

3 结论与讨论

稻瘟病是危害最严重的水稻病害之一, 培育和推广抗病品种是目前最科学的防治对策。由于稻瘟病菌变异频率较高, 大部分抗病品种的抗性会随着应用时间的增长而逐渐降低直至消失^[17]。因此, 需要不断挖掘、鉴定新的抗病品种进行推广或作为抗源应用于未来的稻瘟病抗性育种中。本文针对具有抗稻瘟病潜力的 5 个主栽多年生稻品种 (系) 的抗性水平进行了初步探究。在田间病情调查中, 这 5 个多年生稻品种 (系) 的病情指数均未达到感病系数, 抗性鉴定中, 这 5 个多年生稻品种 (系) 对接种稻瘟病菌为完全免疫反应。因此, 可以认为这些多年生稻抗稻瘟病。此次多年生稻田间抗性的评价是针对其自然状态下的发病情况来评定, 反应了多年生稻在田间的自然抗性的差异, 今后可以进一步建立病圃对多年生稻的抗病水平进行更精准的评定。除此之外, 对多年生稻抗性水平的全面解析还需进一步利用更多的优势生理小种对其抗谱进行测定, 并结合田间鉴定。

多年生稻亲本的田间病情调查结果和抗性鉴定均显示, 长雄野生稻为抗性品种, RD23 为感病品种, 多年生稻的稻瘟病抗性可能来源于父本长雄野生稻。且有前人报道, 基于长雄野生稻转录组中发现大量导致栽培稻感稻瘟病的基因在长雄野生稻中没有检测到相应的基因信号, 长雄野生稻可能是稻瘟病抗性基因库^[18]。本文利用功能性分子标记和紧密连锁 SSR 标记对多个稻瘟病抗性基因在多年生稻品种 (系) 的分布及遗传背景进行分析, 发现 3 个抗性基因位点 *Pish*、*Pita-2*、*Pi5* 可能为多年生稻中来源于长雄野生稻的抗性基因。另外, 本研究中还发现部分多年生稻的稻瘟病抗性可能

来源于长雄野生稻中其余已知基因或未知基因, 这些未知基因很可能是长雄野生稻中未被挖掘的稻瘟病抗性新基因, 需进行更深入的研究。

无论是田间自然发病、接种鉴定, 还是鉴定部分已知的稻瘟病抗性基因或位点, 均表明已经育成的多年生稻 23、云大 24、云大 25、云大 101、云大 107 具有较好的稻瘟病抗性, 这对多年生稻的示范推广、品种布局、植保技术等示范推广具有实际指导意义。

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Evaluation of Rice Blast Resistance in Perennial Rice

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Abstract: Perennial rice has been developed successful by utilizing the rhizome trait of the wild rice species, *Oryza longistaminata* and demonstrated widely, exhibiting broad-spectrum resistance to rice blast. To understand the reason of resistance to blast of perennial rice, disease investigation in farmer's field, inoculation identification and molecular detection of rice blast resistant genes were carried out among nine accessions including five perennial rice varieties (lines) as Perennial Rice 23 (PR23), Yunda24 (PR24), Yunda25 (PR25), Yunda101 (PR101), Yunda107 (PR107), male parent *O. longistaminata*, female parent RD23, F₁(RD23/*O. longistaminata*) and Lijiangxintuanheigu (LTH). The results showed that all the five perennial rice varieties (lines), their male parent *O. longistaminata* and the original F₁ (RD23/*O. longistaminata*) had high resistance to rice blast, while their female parent RD23 showed high susceptibility, which indicated that the rice blast resistance gene of these five perennial rice lines may originated from *O. longistaminata*. The resistance of PR23 and PR25 might owing to the *Pi5* gene and *Pita-2* locus from *O. longistaminata*, and the resistance of PR24 might due to the *pita-2* locus from *O. longistaminata*, while that of PR107 might inherited from *O. longistaminata* with the *Pi5* gene and *Pish* locus. However, none of the known rice blast resistance genes or loci mentioned in this study were harbored by PR101, speculated that the unknown genes from *O. longistaminata* inherited by PR101 archived its blast resistance. The results of this study provided a basis and strategy for blast disease resistance breeding, perennial rice varieties distribution and plant protection technology decision in future.

Key words: perennial rice; rice blast; resistance evaluation; *Oryza longistaminata*

(上接第 8 页)

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Analysis of Characteristics of Temporal and Spatial Variation of Rice Production in the World

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Abstract: The average annual growth rate of rice area, yield per unit area and total yield per unit area increased by 0.67%, 1.65% and 2.33%, respectively, according to the analysis of global rice production from 1961 to 2018. Rice is cultivated in the continents of Asia, Africa, America, Europe and Oceania. Among the rice planting areas in the world, Asia accounts for 87.9%, Africa accounts for 7.7%, America accounts for 4.0%, and Europe and Oceania account for less than 0.5%. Compared with the 1960S, the global rice planting area and the distribution of total rice production in the near 10 years have changed. The harvest area of rice in Africa has increased, and the harvest area of rice in Asia has decreased. Global rice yield growth factor analysis showed that 60% to 70% of the total yield growth was contributed from the increase of yield per unit area. The contribution factors of total rice production growth varied greatly among different continents.

Key words: rice; yield; growth rate; temporal and spatial distribution; world

多年生稻白叶枯病抗性评价

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摘要:利用长雄野生稻地下茎无性繁殖特性培育多年生稻已经成功,并在生产上进行了示范推广。为明确多年生稻品种(系)对白叶枯病的抗性表现,通过田间病情调查、抗性水平鉴定和水稻白叶枯病抗性基因检测3种方法,对多年生稻品种(系)多年生稻23(简称PR23,下同)、云大24(PR24)、云大25(PR25)、云大101(PR101)、云大107(PR107)及其父本长雄野生稻、母本RD23和F₁(RD23/长雄野生稻)的白叶枯病抗性进行评价。结果表明,长雄野生稻高抗白叶枯病;尽管PR23、PR24、PR25、PR107携带白叶枯病抗性基因Xa1、Xa4、Xa23、xa25的等位基因,但在田间自然发病条件下均易感白叶枯病,说明这几个抗性基因对这4个多年生稻品种(系)不起抗病作用;而PR101在田间自然发病条件下表现为抗白叶枯病,并含有白叶枯病抗性等位基因xa25、Xa27,说明这2个基因可能是PR101抗白叶枯病的基因。本研究结果为明确多年生稻对白叶枯病菌的抗病反应,以及抗白叶枯病育种和多年生稻生产布局提供了一定依据。

关键词:多年生稻;白叶枯病;抗性评价

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多年生稻是指种植一次可以连续收获多年(季)的水稻,即从第2年(季)起不再需要买种、育秧、犁田耙田、栽秧等生产环节,大大减少了劳动力投入和减轻了劳动强度,是一项轻简化的稻作生产技术。该项技术包括了多年生稻品种及配套的耕作栽培技术^[1-2]。近年来,云南大学已成功利用长雄野生稻(*Oryza longistaminata*)地下茎无性繁殖特性培育出多年生稻品种^[1-3]。其中,多年生稻23(PR23)已通过云南省审定(审定编号:滇审稻2018033号),云大24(PR24)、云大25(PR25)、云大101(PR101)、云大107(PR107)等品系也开始试验试种。通过前期在云南省内多年多点试验结果来看,尽管多年生稻品种(系)的父本长雄野生稻携带有水稻白叶枯病抗性基因Xa21^[4-5],但多年生稻品种(系)在各地的白叶枯抗性表现不一。多年生稻品种(系)是否具备白叶枯病抗性并携带相关抗病基因并不十分清楚,导致在多年生稻抗白叶枯病育种和生产应用上指导性不强。

因此,本研究通过田间病情调查、人工接种抗性水平鉴定和抗性基因检测3种方法,对多年生稻品种(系)PR23、PR24、PR25、PR101、PR107及其亲本长雄野生稻、RD23和F₁(RD23/长雄野生稻)进行白叶枯病抗性鉴定,以明确多年生稻品种(系)的白叶枯病抗性水平,为今后多年生稻遗传育种、生产防控,以及产业布局提供一定科学依据。

1 材料与方法

1.1 试验材料

以PR23、PR24、PR25、PR101、PR107、长雄野生稻(多年生稻的父本)、RD23(多年生稻的母本)、F₁(RD23/长雄野生稻)共计8个材料进行白叶枯病抗性鉴定。其中,长雄野生稻来源于非洲尼日尔,RD23是泰国优质籼稻,杂交后通过幼胚挽救技术获得了F₁植株,经过多世代的自交,选育出PR23、PR24、PR25、PR101、PR107等多年生稻品种(系)。

1.2 试验地点

试验材料于2019年种植于西双版纳州多年生稻育种基地,海拔为580 m,年平均气温22.6℃,年降水量1200 mm。西双版纳州气候高温高湿,水稻生产易感染白叶枯病。田间调查在西双版纳傣族自治州示范推广田块进行。

1.3 田间管理

接种用品种(系)7月15日播种,8月5日移栽大田,每个品种栽4行,移栽行株距为20 cm×20 cm,单苗移栽,每行10株。示范田早稻播种期为1月15日,移栽期为3月1日,晚稻播种期和移栽期与接种用品种

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· 63 ·

表 1 水稻白叶枯病分级和评价标准

病级	抗性反应	标准评价
0	剪口处无病斑	高抗(HR)
1	剪口处有小病斑, 长度不超过 2 cm	抗(R)
3	病斑下延伸 2 cm 以上, 不超过叶长的 1/4	中抗(MR)
5	病斑占叶面积 1/4 以上至 1/2	中感(MS)
7	病斑长度占叶面积 1/2 以上至 3/4	感(S)
9	病斑长度超过叶片的 3/4	高感(HS)

表 2 PCR 鉴定所用引物序列

抗病基因	正向引物(5'-3')	反向引物(5'-3')	片段大小/bp		退火温度 /°C	参考文献
			抗病	感病		
<i>Xa1</i>	ACTGCCCTCTTGCACACGCCATTGG	CCGGTACATCAGTATTGTCCATCGG	552		58	[11]
<i>Xa3/Xa26</i>	ATGGCTTGACCTAAGTGGA	TGTTCTGAGTGCAGGAGTG	1 100		55	[11]
<i>Xa4</i>	ATCGATCGATCTTCACGAGG	TGCTATAAAAAGCCATTCGGG	157		61	[12]
<i>xa5</i>	CCGGAGCTCGCCATTCAAGTTCTTG	TGCTCTTACTTGGTTCTCC	145	170	53	[13]
<i>Xa10</i>	CATTAGCAGAGCCGAAACTC	ATGAAACGAAACGGTCAAACA		540	59	[14]
<i>xa13</i>	AGCTCCAGCTCTCCAAATG	GGCCATGGCTCAGTGTAT	1 000	280	57	[15]
<i>Xa21</i>	CGATCGGTATAACAGCAAAAC	ATAGCAACTGATTGCTTGG	1 400	1 300	58	[16]
<i>Xa23</i>	TAAGTTCTACATCGACCCCA	CACATGAAGAGCTGGAAAGG		760	58	[17]
<i>xa25</i>	TTCTGTTCCTGTGGCTTTG	TGGATCACTCGCTTCTGCA	930	860	55	[18]
<i>Xa27</i>	TAGTGTCTAAATACAGGGACT	GAGTACTTGTCTGATGCTC	149	174	54	[19]

一致, 移栽行株距为 20 cm×20 cm, 每丛栽 1~2 苗。接种田和示范田田间水肥管理参照当地大面积水稻生产田。

1.4 白叶枯病抗性鉴定

1.4.1 田间病情调查

6 月、10 月对西双版纳州试验田及示范推广田块的 PR23、PR24、PR25、PR101、PR107, 以及长雄野生稻、RD23 和 F₁(RD23/长雄野生稻) 进行早稻和晚稻的田间白叶枯病病情调查, 采用五点取样调查法, 病级评价参照已有标准^[6](表 1)。

1.4.2 田间接种鉴定

选取 9 个不同致病力的水稻白叶枯病生理小种用于抗性水平鉴定, 即 YP1、YP2、YP3、YP4、YP5、YP6、YP7、YP8、YP9 菌株(由云南农业大学植物病理研究室分离鉴定并提供)。其中, YP1 为弱致病力菌株, YP6 为强致病力菌株。病原菌分别于 PSA 培养基(马铃薯 200 g, 葡萄糖或蔗糖 20 g, 琼脂 15~20 g, 蒸馏水 1 000 mL)上 30℃ 培养 72 h 后, 配制 3×10⁸ CFU/mL 菌液备用。选取生长时期一致的多年生稻叶片, 于 15:00、温度为 28℃~30℃ 时, 采用剪叶法接种^[7], 即剪去叶尖 1~3 cm 进行伤口接种。每个菌株接种 4 个植株, 每个植株接种 3~5 个叶片(剑叶和上 3 叶)。接种 21 d 后调查白叶枯病发病情况。

1.4.3 抗性基因检测

1.4.3.1 DNA 制备 取 0.1 g PR23、PR24、PR25、PR101、PR107、长雄野生稻、RD23、F₁(RD23/长雄野生稻) 的幼嫩叶片, CTAB 法^[8]提取其基因组 DNA, 置于 -20℃ 冰箱保存备用。

1.4.3.2 PCR 鉴定 基于已报道和克隆的 10 个抗白叶枯病基因, 包括 7 个显性抗病基因(*Xa1*、*Xa3*、*Xa4*、*Xa10*、*Xa21*、*Xa23*、*Xa27*) 和 3 个隐性抗病基因(*xa5*、*xa13*、*xa25*)。利用已发表的功能标记或分子标记进行 PCR 扩增(表 2), 利用聚丙烯酰胺凝胶电泳^[9]和 1%~2% 的琼脂糖凝胶电泳^[10]对 PCR 产物进行检测。

2 结果与分析

2.1 田间病情调查

从表 3 可见, 长雄野生稻、F₁、PR101 在早、晚稻全生育期对白叶枯病均表现出中抗以上抗性水平; RD23 在早稻全生育期表现出中抗以上抗性水平, 在晚稻的分蘖期和孕穗期表现出中感和感(表 3); 5 个多年生稻品种(系)均不同程度感白叶枯病, 其中, PR107 感病最严重, 在早、晚稻苗期、分蘖期和孕穗期均表现出感病。

2.2 抗性水平评价

从供试菌种看, YP6 菌株致病力最强, 除了长雄野生稻外, 能使多年生稻品种(系)以及 RD23 和 F₁ 均感病; YP1 菌株致病力相对最弱, 8 个材料均对其表现出抗性(表 4)。

表 3 多年生稻白叶枯病田间病情调查结果

季节	时期	长雄野生稻	RD23	F ₁	PR23	PR24	PR25	PR101	PR107
早稻	苗期	HR	R	R	R	R	R	R	MS
	分蘖期	R	R	R	MS	R	MS	R	MS
	孕穗期	R	MR	MR	MS	MS	MS	R	S
晚稻	苗期	HR	R	R	R	R	R	R	MS
	分蘖期	R	MS	MR	MS	MS	MS	R	S
	孕穗期	R	S	MR	S	S	S	MR	HS

表 4 多年生稻品种(系)及其亲本和 F₁ 田间病情调查和抗性水平评价结果

供试菌种	长雄野生稻	RD23	F ₁	PR23	PR24	PR25	PR101	PR107
田间自然发病	R	S	MR	S	S	S	MR	HS
YP1	R	R	R	MR	MR	R	MR	MR
YP2	R	R	MR	MR	MR	MR	R	S
YP3	R	MR	MR	MR	MR	MR	MR	MS
YP4	HR	MR	R	MR	R	MR	R	S
YP5	R	MS	R	MR	MR	MR	MR	MS
YP6	MR	MS	MS	S	MS	S	MS	S
YP7	R	R	R	MS	MS	MS	R	S
YP8	R	R	MR	MS	MS	MS	MR	MS
YP9	MR	MS	MS	S	MS	MS	MR	S

表 5 白叶枯病抗性基因在多年生稻品种(系)中的分子检测结果

分子标记	长雄野生稻	RD23	F ₁	PR23	PR24	PR25	PR101	PR107
<i>Xa1</i>	+	+	+	+	+	+	+	+
<i>Xa3/Xa26</i>	-	-	-	-	-	-	-	-
<i>Xa4</i>	+	+	+	+	+	+	+	+
<i>xa5</i>	-	-	-	-	-	-	-	-
<i>Xa10</i>	-	-	-	-	-	-	-	-
<i>xa13</i>	-	-	-	-	-	-	-	-
<i>Xa21</i>	+	-	-	-	-	-	-	-
<i>Xa23</i>	+	-	+	+	-	+	-	-
<i>xa25</i>	-	-	+	-	-	-	+	-
<i>Xa27</i>	+	-	+	-	-	-	+	-

“+”表示携带检测基因;“-”表示不携带检测基因。

从多年生稻品种(系)看,长雄野生稻对 9 个供试菌种均表现出抗病;PR101 对 YP6 菌株表现为中感,但对其他 8 个菌株均表现为中抗以上;PR23、PR24 和 PR25 对 9 个菌株具有不同的抗性表现,对 YP6、YP7、YP8、YP9 菌株的感病程度与田间病情调查结果一致;PR107 对除 YP1 外的 8 个菌株均表现出感病(表 4)。

不同致病力生理小种的抗性水平鉴定结果虽然与田间调查结果存在一定差异,但感抗病情况基本吻合,说明该抗性水平评价结果可以直接指导田间白叶枯病害防治。

2.3 抗病基因检测

检测结果(表 5)发现,长雄野生稻、RD23、F₁、PR23、PR24、PR25、PR101 和 PR107 具有 *Xa1*、*Xa4*、*Xa23* 和 *xa25* 等位基因,说明这些材料具有潜在的 *Xa1*、*Xa4*、*Xa23*、*xa25* 抗性基因。田间病情调查结果(表

4) 表明, RD23、PR23、PR24 和 PR25、PR107 均感白叶枯病,而长雄野生稻、F₁ 和 PR101 均抗白叶枯病,说明 RD23、PR23、PR24、PR25、PR107 携带的为感病等位基因,长雄野生稻、F₁、PR101 可能携带部分相关基因的抗病等位基因。

Xa3/Xa26 基因的功能标记检测显示,在长雄野生稻、RD23、F₁、PR23、PR25、PR101 和 PR107 都未扩增出基因条带,推测长雄野生稻、RD23、F₁、PR23、PR25、PR101 和 PR107 中可能不携带 *Xa3/Xa26* 基因。*Xa21* 基因的功能标记检测显示,只有长雄野生稻中扩增出抗病基因带型,而在 RD23、F₁、PR23、PR25、PR101 和 PR107 扩增出感病基因带型,PR24 中未扩增出条带,推测 *Xa21* 基因虽然是来源于长雄野生稻的白叶枯病抗性基因,但是没有遗传到其衍生的多年生稻品种(系)中。白叶枯病抗性基因 *xa25* 在 RD23、PR23、

PR24、PR25 和 PR107 中为感病基因型 (860 bp), 且 RD23、PR23、PR24、PR25 和 PR107 均感白叶枯病, 而在 F₁ 和 PR101 中为抗病基因型(约 930 bp), 推测 *xa25* 可能在 F₁ 和 PR101 的抗白叶枯病中起到了积极作用。*Xa27* 基因功能标记检测表明, 在长雄野生稻、F₁ 和 PR101 中扩增出了抗病基因带型, PR107 中未扩增出条带, 在 RD23、PR23、PR24、PR25 扩增出感病基因带型, 这与长雄野生稻、F₁、PR101 在田间病情调查结果相符, 说明 PR101 可能携带 *Xa27* 抗病基因, 起到主要抗病作用。

PR23、PR24、PR25 和 PR107 携带已知的白叶枯病抗性基因 *Xa1*、*Xa4*、*Xa23*、*xa25* 的等位基因, 但均感病, 说明这几个抗病等位基因在这些材料中为感病基因型; 虽然长雄野生稻携带已知白叶枯病抗性基因 *Xa1*、*Xa4*、*xa25*、*Xa21*、*Xa23*、*Xa27*, 但从其 F₁ 及衍生的 5 个多年生稻品种 (系) 的田间病情调查结果和携带基因看, *Xa27* 和 *xa25* 基因可能是由长雄野生稻遗传给 PR101 并赋予其白叶枯病抗性的主要原因。

因此, PR101 抗白叶枯病是由于其可能携带来自长雄野生稻的 *Xa27*、*xa25* 基因, 而 PR23、PR24、PR25 和 PR107 这 4 个多年生稻品种 (系) 不具备本研究中用到的 10 个抗白叶枯病基因。

3 结论和讨论

白叶枯病在籼稻和粳稻中发病情况具有一定差异, 一般籼稻重于粳稻, 晚稻重于早稻^[20]。根据对不同致病力白叶枯病菌生理小种抗性水平鉴定发现, PR101 对大部分白叶枯病生理小种表现出抗性, 并与田间生产条件下表现一致; PR23、PR24 和 PR25 仅对部分白叶枯病生理小种具有抗性, 需要进一步进行白叶枯病抗性遗传改良; PR107 对大部分白叶枯病生理小种均感病, 是制约其推广应用的主要限制因素, 急需进行白叶枯病的抗性改良。

多年生稻 PR23、PR24、PR25、PR101 和 PR107 中均不含 *xa5*、*Xa3*/*Xa26*、*xa13*、*Xa10*、*Xa21* 抗病等位基因。PR23、PR24、PR25 和 PR107 携带白叶枯病抗性位点基因 *Xa1*、*Xa4*、*Xa23*、*xa25*, 但根据田间病情调查发现这几个品系均感病, 说明 *Xa1*、*Xa4*、*Xa23*、*xa25* 抗性位点基因在 PR23、PR24、PR25、PR107 中不起抗病作用; 在长雄野生稻中检测到携带有 *Xa1*、*Xa4*、*Xa21*、*Xa23*、*xa25* 和 *Xa27* 等白叶枯病抗性位点基因, 但从其 F₁ 及衍生的 5 个多年生稻品种 (系) 的田间病情调查结

果和携带基因看, *xa25*、*Xa27* 基因可能是通过长雄野生稻遗传到 PR101 的白叶枯病抗性位点基因。

xa25 是一个隐性的抗白叶枯病主效基因, 与其对应的显性基因是 *Xa25*。*xa25* 的供体品种是明恢 63, 对白叶枯菌生理小种 PXO339 表现为专化性抗性^[21]。由于 *xa25* 的启动子突变, 导致 PthXo2 无法被识别, 则其表达便不受诱导, 表现为抗性^[22-23]。*xa25* 的表达受显性等位基因 *Xa25* 的调控。王石平等^[24]通过转基因技术将 *xa25* 的部分 DNA 片段导入到水稻品种中, 抑制其表达从而增强水稻品种的抗性。所以猜想 PR101 可能是由于抑制了 *xa25* 的表达而表现为抗白叶枯病。

已有报道, 白叶枯病抗性位点基因 *Xa27* 来自小粒野生稻 (*O. minuta*)^[17,25], 而来源于长雄野生稻的 *Xa27* 等位基因也可能是白叶枯病的抗性位点基因。WU 等^[26]发现, *Xa27* 的表达是通过增加叶片维管束次生细胞壁厚度来抵御病原菌的侵染, 推测 PR101 能抵抗白叶枯病可能是通过增加维管束次生细胞壁的厚度来抵御侵害。

多年生稻 PR101 对白叶枯病表现出良好抗性, 可作为改良水稻抗白叶枯病的基因库。深入研究多年生稻 PR101 对白叶枯病的抗性反应, 有助于水稻白叶枯病抗病育种研究, 拓宽水稻抗白叶枯病育种的材料基础; 而在利用 PR23、PR24、PR25 和 PR107 进行稻作生产时, 需要注意及时有效的进行白叶枯病防治。

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Identification of Bacterial Blight Resistance in Perennial Rice

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Abstract: Perennial rice (PR), using vegetative propagation via Rhizome as perenniality donor from *Oryza longistaminata*, has been bred successfully and demonstrated widely. In order to clarify the resistance performance of perennial rice varieties (lines) to bacterial leaf blight, the perennial rice varieties (lines) PR23, PR24, PR25, PR101, PR107, and their male *Oryza longistaminata*, female parents RD23 and F₁ (RD23/*Oryza longistaminata*) were used as the materials to evaluate their resistance to bacterial blight by three methods: field disease investigation, resistance level identification and rice bacterial blight resistance gene detection. The results showed that, *O. longistaminata* presents high resistance to bacterial blight. Although PR23, PR24, PR25, PR107 carry the alleles of bacterial blight resistance genes *Xa1*, *Xa4*, *Xa23*, *xa25*, but they are all susceptible to bacterial blight in the field. It shows that these resistance genes do not play a role in disease resistance in these four perennial rice varieties (lines). PR101 shows resistance to bacterial blight under natural disease conditions in the field, and contains the bacterial blight resistance alleles *xa25*, *Xa27*, indicating that these two genes may be PR101 resistance genes to bacterial blight. The results provided a basis and strategy for both bacterial blight resistance breeding and application of perennial rice in future.

Key words: perennial rice; bacterial blight; resistance evaluation

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一种两收模式下多年生稻产量潜力初探

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摘要: 以多年生稻品系 PR25 和再生稻品种渝梗优 5029 (RR1)、甬优 1540 (RR2)、佳辐占 (RR3)、宜优 673 (RR4)、内优 7075 (RR5) 为材料, 采用单因素试验探讨多年生稻与再生稻产量、产量构成、生育期、SPAD、根系活力等性状的异同。结果表明: PR25 产量与再生稻相比, 头季持平或者略低, 第二季 PR25 产量为 471.10 kg/667m², 显著高于所有再生稻品种, 较 RR1、RR2、RR3、RR4 和 RR5 分别增产 48.22%、34.79%、60.95%、31.71%、45.58%; 周年产量 PR25 为 1 031.63 kg/667m², 亦显著大于再生稻品种, 较 RR1、RR2、RR3、RR4 和 RR5 分别增产 5.82%、10.41%、47.00%、13.19% 和 42.66%。多年生稻 PR25 再生季的周年产量较再生稻高的主要原因是: 多年生稻再生季的单位面积颖花数、有效穗数和结实率均高于再生稻的再生季; PR25 头季齐穗后剑叶 SPAD 衰减幅度较小, 剑叶具有较强的光合能力, 头季成熟期根系维持在较高活力水平且再生能力较强; 多年生稻再生季营养生长期至营养生长与生殖生长并进期明显长于再生稻, 进而全生育期较再生稻呈延长趋势, 利于干物质积累。
关键词: 多年生稻; 再生稻; 产量及其构成; 产量潜力

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Preliminary Study on Yield Potential of Perennial Rice Under Two-Harvest Model

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Abstract: A single factor experiment was conducted to investigate the differences of yield, yield components, growth period, SPAD and root activity between the perennial rice line PR25 and the ratooning rice varieties Yujingyou 5029 (RR1), Yongyou 1540 (RR2), Jiafuzhan (RR3), Yiyou 673 (RR4) and Neiyou 7075 (RR5). The results showed that: (1) the yield of PR 25 in the first season was approximate to or slightly lower than those of the ratooning rice varieties; in the second season, PR25 yielded 7 066.5 kg/hm², which was 48.22%, 34.79%, 60.95%, 31.71% and 45.58% higher than RR1, RR2, RR3, RR4 and RR5, respectively, reaching the significant levels; the annual yield of PR25 was 15 474.45 kg/hm², 5.82%, 10.41%, 47.00%, 13.19% and 42.66% higher than that of RR1 RR2, RR3, RR4 and RR5, respectively, reaching significant increases; (2) the main reason why the annual yield of PR25 in ratooning season was higher than that of ratooning rice was that the number of spikelets per unit area, effective panicles and seed setting rate of PR25 were higher than those of ratooning rice; after full heading, the flag leaf of PR25 had a strong photosynthetic capacity with a slight decrease of SPAD value; at the maturity period of the first season, PR25 maintained a high root activity and a strong regeneration ability; the period from vegetative growth to vegetative-reproductive growth of perennial rice was significantly longer than that of ratooning rice, furthermore, the whole growth period of perennial rice was longer than that of ratooning rice, which was beneficial to dry matter accumulation.

Key words: perennial rice; ratooning rice; yield and its composition; yield potential

再生稻是通过一定的栽培管理措施, 使头季稻收割后稻桩上的休眠芽继续萌发生长成穗而收获的一季水稻。再生稻具有生育期短、日产量较高、省种省工节水、生产成本低和效益高等优点, 是南方稻区种植一季稻热量有余而种植双季稻热量又不足的稻田提高复种指数、增加单位面积稻谷产量和经济收入的有效措施之一^[1]。多年生稻为收割后, 留下的稻桩安全越冬, 第二季或第二年通过栽培手段使其再萌发成

苗, 形成新的稻株, 如此周而复始, 实现水稻一次种植、多(季)年收获, 双季稻区可一年收 2 季, 一季稻区一年收获 1 季, 可以实现多年连续收获; 种植多年生稻具有省种、省工等节本增效的优点^[2]。Hu 等^[3]在解析长雄野生稻地下茎无性繁殖特性遗传规律基础上, 利用长雄野生稻无性繁殖特性成功培育出系列多年生稻品种(系), 包括多年生稻 23 (PR23)、PR25、PR107 等品种(系)。其中, PR23 在云南和老挝试种, 表现出广泛的适应性和较强的多年生性^[4], 并在 2018 年通过云南省审定, 在云南不同生态区种植, 产量在年份间基本稳定, 与当地常规稻品种产量基本持平, 米质受大米加工企业和广大消费者喜爱。多年生稻从

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第二季起,省去买种、育秧、犁田、耙田、移栽等环节,与再生稻相比可以更加节约生产成本,大幅度提高效益^[5],目前在云南适宜地区已经开始推广种植。而多年生稻品系 PR25,比 PR23 多年生性更强、米质更优。

研究表明,从头季稻收割后到再生稻成熟生育期仅 60 d 左右,与同期抽穗主季稻源库流相比,再生稻叶面积指数为主季稻的 1/8~1/5,穗粒数和产量为主季稻的 1/3 左右,但齐穗至齐穗后 10 d 再生稻光合速率较主季稻高 20%~70%,孕穗至成熟期再生稻净同化率是主季稻的 2.7~6.0 倍^[6]。成熟期单茎鞘干质量大、茎鞘物质输出率高,有利于再生稻的高产^[7]。徐富贤等^[8]研究指出,头季稻齐穗到成熟叶片 SPAD 值衰减指数可作为鉴定再生力的指标。郑景生等^[9]认为再生季稻再生分蘖的生育依赖于头季稻残留的根系,再生季稻穗数及产量与头季稻成熟期和再生季稻齐穗期根系活力呈极显著线性正相关。因此,头季稻成熟期根系伤流量可作为诊断再生力、筛选再生稻品种的重要指标。由此可知,再生稻头季成熟期物质积累、产量构成、剑叶 SPAD 值、根系伤流与再生季产量等再生指标密切相关。研究以多年生稻品系 PR25 和再生稻品种渝粳优 5029 (RR1)、甬优 1540 (RR2)、佳辐占 (RR3)、宜优 673 (RR4)、内优 7075 (RR5) 为材料,采用单因素试验探讨多年生稻与再生稻产量、产量构成、生育期、SPAD、根系活力等性状的异同,以期为多年生稻栽培生理基础研究和生产应用提供理论依据。

1 材料与方法

1.1 供试材料

供试材料为多年生粳稻品系 PR25 和再生稻品种渝粳优 5029 (RR1)、甬优 1540 (RR2)、佳辐占 (RR3)、宜优 673 (RR4)、内优 7075 (RR5),共 6 个水稻品种(系)。

1.2 试验设计

试验于 2018 年 4—12 月在云南省西双版纳傣族自治州景洪市勐龙镇进行,试验田地东经 100°39'47",北纬 21°33'34",海拔高 666 m。采用单因素随机区组设计,每个品种(系)设 3 个重复,共 18 个小区,小区面积 20 m²,四周设保护行 4 行以上。

1.3 田间操作与管理

各品种(系)均于 2018 年 4 月 8 日播种,5 月 7 日移栽,株行距 20 cm × 25 cm,第一季收割后蓄留稻桩高度均为 5 cm。头季肥料纯氮用量为 12 kg/667m²,氮、磷、钾施用比例为 2:1:2,其中,氮肥按基肥:分蘖肥:穗肥:保根肥=3:3:2:2 施用,磷肥全部作基肥施,钾肥按基肥:穗肥:保根肥=4:4:2 施用;保根肥为头季稻齐穗后 20 d 左右施入。第二季肥料的纯氮用量和氮、磷、钾比例与头季相同,其中,氮肥

按基肥:分蘖肥:穗肥=5:3:2 施用,磷肥全部作基肥施,钾肥按基肥:穗肥=1:1 施用。水分管理:寸水活棵、浅水分蘖、够苗晒田,拔节抽穗期保持田间有水、干湿交替壮籽。移栽后 5~7 d 施用丙草胺、苄嘧磺隆等常规除草剂除草;在苗期到幼穗分化期做好稻飞虱、南方黑条矮缩病防治,分蘖盛期和破口期做好稻飞虱、稻纵卷叶螟、纹枯病、白叶枯病的防治。

1.4 测定项目与方法

1.4.1 SPAD 值衰减率 于头季稻齐穗后 10 d 和成熟期,用 SPAD 仪测定剑叶 SPAD 值,直到成熟收割为止。SPAD 衰减率=(成熟期 SPAD-齐穗后 10 d SPAD)/齐穗后 10 d SPAD。

1.4.2 根系活力测定 头季成熟期测定根系伤流量,每个小区测定 3 株。具体操作:第 1 天 19:00,在离地面 10 cm 处割出伤口,用封口袋装脱脂棉连接在伤口处,次日早上 8:30 收回,测定脱脂棉重量,计算单株单位时间伤流量。

1.4.3 生育期记载 记载头季播种期、移栽期、齐穗期、成熟期及收获期,再生季齐穗期和成熟期的具体时间。

1.4.4 产量及产量构成 头季每个小区取 12 株进行考种,测定结实率、千粒重、每穗粒数,每个小区数 30 株有效穗,计算理论产量,同时每个小区取 5 m² 进行实割测产;再生季取 12 株进行考种,考察不同节位有效穗、结实率、千粒重,计算单株产量及不同节位对产量贡献率,同时每个小区取 5 m² 进行实割测产。

1.4.5 干物质积累 于齐穗期和成熟期取样,每小区取 3 株,洗净泥沙,测定茎蘖数,然后去根,将样品分成茎、叶、穗 3 部分(成熟期将样品分成稻草、枝梗、实粒、秕粒 4 个部分),于 105℃ 杀青 20 min,然后在 80℃ 下烘 48 h 以上,冷却至恒温称干物重。

1.5 数据分析

数据采用 Excel 和 SPSS 23 软件进行整理分析。

2 结果与分析

2.1 多年生稻和再生稻产量及产量构成特点分析

如表 1 所示,头季产量为 RR1 > RR2 > PR25 > RR4 > RR3 > RR5,其中 RR1 产量最高为 657.07 kg/667m²,RR2 次之为 584.83 kg/667m²,PR25 排第三,其中 PR25 与 RR2 和 RR4 差异不显著,但显著 ($P < 0.05$) 高于 RR3 和 RR5;再生季产量 PR25 为 471.10 kg/667m²,显著高于所有再生稻品种,较 RR1、RR2、RR3、RR4 和 RR5 分别增加 48.22%、34.80%、60.95%、31.71%、45.58%,周年产量 PR25 为 1 031.63 kg/667m²,亦显著高于再生稻品种,较 RR1、RR2、RR3、RR4 和 RR5 分别增加 5.82%、10.41%、47.00%、13.19%、42.66%。

再生稻品种头季产量和周年产量均以 RR1 最高，分别为 657.07 和 974.90 kg/667m²，而再生季产量 RR4 最高，为 357.67 kg/667m²。可以看出，PR25 产量与再生稻相比头季持平或者略低，但再生季和周年产量显著超过再生稻品种。

表 1 多年生稻和再生稻产量差异比较 (kg/667m²)

品 种	头季产量	再生季产量	周年产量
PR25	560.50 ± 27.58 b	471.10 ± 20.68 a	1 031.63 ± 34.00 a
RR1	657.07 ± 49.14 a	317.83 ± 8.80 c	974.90 ± 49.23 b
RR2	584.83 ± 11.74 b	349.50 ± 8.89 b	934.33 ± 10.60 bc
RR3	409.10 ± 12.96 c	292.70 ± 0.72 d	701.78 ± 18.76 d
RR4	553.80 ± 20.30 b	357.67 ± 10.71 b	911.43 ± 18.65 c
RR5	399.57 ± 1.43 c	323.60 ± 10.12 c	723.16 ± 23.69 d

注：同列不同小写字母表示差异显著 (P<0.05)，下同(有季别的为同季比较)。

如表 2 所示，总的来看，再生季与头季比，颖花数、每穗粒数、千粒重有所降低，而有效穗数和结实率均有所增加。头季单位面积颖花数为 RR2 > RR4 >

PR25 > RR1 > RR5 > RR3，每穗粒数为 RR2 > RR4 > RR1 > PR25 > RR5 > RR3，千粒重为 RR4 > RR3 > RR5 > RR1 > PR25 > RR2，有效穗数为 PR25 > RR1 > RR3 > RR5 > RR4 > RR2，结实率为 RR1 > RR3 > PR25 > RR2 > RR5 > RR4 >，头季 PR25 产量构成各因素与头季产量趋势基本一致。PR25 再生季单位面积颖花数、有效穗数和结实率均大于再生稻，其中颖花数较 RR1、RR2、RR3、RR4 和 RR5 分别增加 10.82%、0.68%、50.76%、35.00%、32.00%，其中除了与 RR2 差异未达显著水平，与其他品种差异均显著；有效穗数分别增加 51.49%、13.34%、6.08%、4.28%、5.52%，除与 RR2 差异显著之外，与其他再生稻差异均不显著；结实率分别增加 35.24%、27.57%、11.62%、17.55%、8.89%，每穗粒数和千粒重均排在第 3。从产量构成因素看，多年生稻再生季产量较再生稻高的主要原因是再生季单位面积颖花数、有效穗数和结实率高于再生稻。

表 2 多年生稻和再生稻产量构成分析

季 别	品 种	颖花数 (×10 ² 朵/m ²)	每穗粒数 (粒)	千粒重 (g)	有效穗数 (穗/m ²)	结实率 (%)
头 季	PR25	393 ± 16.86 b	145 ± 20.40 c	27.83 ± 0.67 d	273.50 ± 26.68 a	76.83 ± 0.46 b
	RR1	388 ± 31.99 b	147 ± 24.30 c	28.47 ± 0.64 cd	269.03 ± 56.73 a	89.37 ± 2.96 a
	RR2	546 ± 16.84 a	261 ± 12.71 a	23.43 ± 1.45 e	210.10 ± 16.68 b	68.67 ± 0.75 c
	RR3	257 ± 9.04 d	109 ± 1.00 d	30.33 ± 0.25 b	235.47 ± 7.52 ab	78.60 ± 1.02 b
	RR4	413 ± 1.43 b	182 ± 4.73 b	33.40 ± 0.02 a	226.80 ± 6.67 ab	60.27 ± 2.45 d
	RR5	325 ± 0.51 c	142 ± 10.50 c	29.47 ± 0.16 bc	230.10 ± 16.68 ab	62.70 ± 1.39 d
再 生 季	PR25	297 ± 15.54 a	88 ± 7.54 b	27.30 ± 0.69 bc	340.20 ± 46.69 a	87.73 ± 1.51 a
	RR1	268 ± 2.39 b	101 ± 3.49 a	25.47 ± 0.40 c	224.57 ± 10.19 b	64.87 ± 6.33 e
	RR2	295 ± 10.04 a	98 ± 3.22 a	25.90 ± 2.06 c	300.17 ± 20.01 a	68.77 ± 1.37 e
	RR3	197 ± 6.21 d	61 ± 1.22 d	28.60 ± 1.48 b	320.70 ± 19.19 a	78.60 ± 0.43 c
	RR4	220 ± 3.72 c	67 ± 0.36 cd	31.13 ± 0.32 a	326.23 ± 5.87 a	74.63 ± 0.53 d
	RR5	225 ± 3.40 c	70 ± 4.42 c	26.80 ± 1.37 bc	322.40 ± 19.25 a	80.57 ± 0.65 b

2.2 多年生稻和再生稻生育期差异分析

各品种再生季全生育期与头季相比均有所缩短，平均缩短 60.7 d，其中齐穗前生育期再生季较头季平均缩短 61.2 d，是造成全生育期缩短的主要原因(表 3)。头季齐穗期在 7 月 5—27 日，成熟期在 8 月 6 日—9 月 1 日，全生育期为 125~151 d，其中 RR5 最长，为 151 d，RR3 最短，为 125 d，各品种生殖生长期(齐穗后)差异不明显，为 31~36 d，PR25 和 RR5 最长，为 36 d；而营养生长期和营养生长与生殖生长并进期(播种至齐穗期)为 93~115 d，是造成全生育期差异的主要阶段。再生季各品种齐穗期为 9 月 6 日—11 月 10 日，成熟期为 10 月 6 日—12 月 15 日，各品种间相差较大；全生期为 PR25 最长为 110 d，较 RR1、RR2、RR3、RR4、RR5 分别延长 36、20、49、41、45 d，再生稻品种全生育期为 61~90 d，其中，PR25 的营养生长期及营养生长与生殖生长并进期(头季收获至再生季齐穗期)为 75 d，较 RR1、RR2、RR3、RR4、RR5

表 3 多年生稻和再生稻生育期比较

季 别	品 种	齐穗期 (月-日)	成熟期 (月-日)	播种/收获—齐穗期 (d)	齐穗—全生育成熟 (d)	全生育期 (d)
头 季	PR25	07-22	08-27	110	36	146
	RR1	07-12	08-14	100	33	133
	RR2	07-24	08-14	102	31	133
	RR3	07-05	08-06	93	32	125
	RR4	07-23	08-26	111	34	145
	RR5	07-27	09-01	115	36	151
再 生 季	PR25	11-10	12-15	75	35	110
	RR1	09-24	10-27	41	33	74
	RR2	10-05	11-12	52	38	90
	RR3	09-06	10-06	31	30	61
	RR4	09-29	11-03	34	35	69
	RR5	10-02	11-05	31	34	65

分别延长 34、23、44、41、44 d，生殖生长期(齐穗后)差异不明显。多年生稻和再生稻品种生育期差异主要在营养生长期，而生殖生长期差异不明显。多年生稻

再生季营养生长期至营养生长与生殖生长并进期明显长于再生稻, 进而全生育期较再生稻明显延长。

2.3 多年生稻和再生稻头季剑叶 SPAD 值及根系活力分析

如图 1 所示, 头季各品种齐穗后 10 d 和成熟期 SPAD 值差异均不显著, 其中, 齐穗后 10 d PR25、RR1、RR2、RR3、RR4、RR5 的剑叶 SPAD 值分别为 38.02、39.06、39.84、39.09、36.77、39.07, 成熟期为 RR2 > PR25 > RR5 > RR1 > RR3 > RR4; 叶面积衰减率为 RR3 > RR1 > RR4 > RR5 > RR2 > PR25, 其中 PR25 衰减率最低为 9.71%, 较 RR3、RR1、RR4、RR5、RR2 分别减少 48.38%、43.50%、32.68%、28.34%、15.86%。灌浆结实期各品种 SPAD 差异不明显, 但是后期 SPAD 衰减率多年生稻低于再生稻, 说明后期多年生稻叶片早衰程度低于再生稻, 剑叶光合持续时间较长。由图 2 可知, 头季成熟期单株根系伤流量表现为 PR25 > RR2 > RR4 > RR5 > RR1 > RR3, 其中 PR25 最大, 为 47.9 mg/h, 较 RR2、RR4、RR5、RR1、RR3 分别增加 5.8%、54.3%、92.2%、124.1%、213.3%, 其中除了与 RR2 差异不显著外, 与其他品种差异均达到显著水平。这说明多年生稻在头季成熟期仍能保持较高的根系活力。

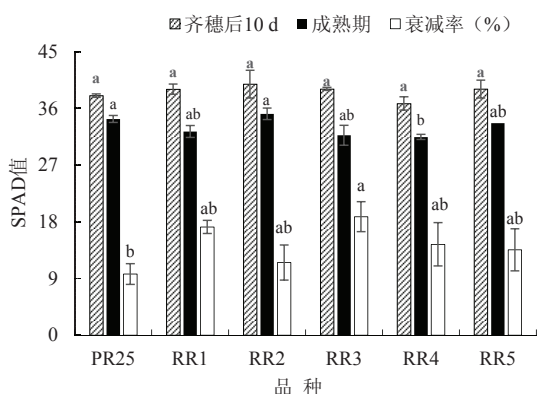


图 1 多年生稻和再生稻剑叶 SPAD 值 [图中不同小写字母表示品种间差异显著 (P < 0.05), 下同]

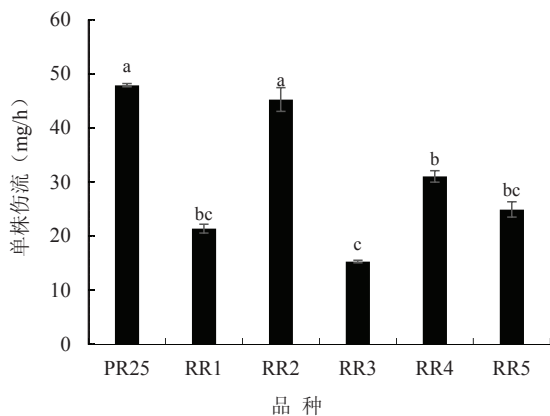


图 2 多年生稻和再生稻的根系伤流量

2.4 多年生稻和再生稻干物质积累分析

再生季与头季比较, 齐穗期和成熟期干物质都

明显减少 (表 4), 头季齐穗期干物质为 RR4 > RR5 > PR25 > RR2 > RR1 > RR3, 其中, RR4 最大, 为 1265.4 g/m², RR3 最小, 为 900.2 g/m², 成熟期为 RR1 > PR25 > PR4 > RR2 > RR5 > RR3, 其中, RR1 最大, 为 1825.0 g/m², RR3 最小, 为 1303.2 g/m²。再生季齐穗期为 RR3 > RR4 > PR25 > RR1 > RR5 > RR2, 成熟期 (不含老稻桩) 为 PR25 显著大于 RR1、RR2、RR3、RR4 和 RR5, 分别增加 39.93%、28.16%、119.17%、26.14% 和 48.69%。再生季与头季相比, 多年生稻干物质下降幅度低于再生稻, 干物质积累量高于再生稻, 是多年生稻产量高于再生稻重要原因之一。

表 4 多年生稻和再生稻干物质积累量分析

品种	头季 (g/m ²)		再生季 (g/m ²)		
	齐穗期	成熟期	齐穗期	成熟期 (含老稻桩)	成熟期 (不含老稻桩)
PR25	1152.2 c	1815.0 a	789.3 b	1742.0 ab	1486.2 a
RR1	942.3 e	1825.0 a	757.3 bc	1257.1 c	1062.1 c
RR2	1107.7 d	1687.8 b	684.2 c	1620.0 ab	1159.6 b
RR3	900.2 f	1303.2 d	982.9 a	1519.8 bc	678.1 e
RR4	1265.4 a	1769.2 ab	868.0 ab	1711.2 ab	1178.2 b
RR5	1226.5 b	1585.3 c	727.0 c	1847.6 a	999.5 d

3 结论与讨论

水稻产量由单位面积内有效穗数、每穗粒数、结实率和千粒重构成, 这 4 个因素对再生稻产量的形成都具有重要作用, 但作用程度存在明显差异^[10]。再生稻头季稻产量与每穗粒数的相关性最密切, 其次为穗数, 头季高产主要是在稳定穗数的基础上主攻大穗, 形成巨大的库容量; 再生季产量与单位面积穗数的相关性最密切, 其次为每穗粒数, 再生季高产应培育更多的穗数, 形成巨大的库容量, 进而获得更高产量^[11-18]。头季产量为 RR1 > RR2 > PR25 > RR4 > RR3 > RR5, 其中 RR1 产量最高, 为 657.07 kg/667m², RR2 次之, 为 584.83 kg/667m², PR25 排第三位, 从产量构成来看, 头季单位面积颖花数为 RR2 > RR4 > PR25 > RR1 > RR5 > RR3, 每穗粒数为 RR2 > RR4 > RR1 > PR25 > RR5 > RR3, 应该说每穗粒数低于 RR2 和 RR1 是产量低于两者的主要原因。再生季产量为 PR25 为 471.10 kg/667m², 显著高于所有再生稻品种, 较 RR1、RR2、RR3、RR4 和 RR5 分别增加 48.22%、34.79%、60.95%、31.71% 和 45.58%, 周年产量 PR25 为 1031.63 kg/667m², 亦显著高于再生稻品种, 较 RR1、RR2、RR3、RR4 和 RR5 分别增加 5.82%、10.41%、47.00%、13.19% 和 42.66%, 再生稻品种头季产量和周年产量均以 RR1 最高, 分别为 657.07 和 974.90 kg/667m², 而再生季产量 RR4 最高, 为 357.67 kg/667m²。再生季 PR25 单位面积颖花数、有效穗数和结实率均大于再生稻, 其中,

颖花数较 RR1、RR2、RR3、RR4 和 RR5 分别增加 10.82%、0.68%、50.76%、35.00% 和 32.00%（除了与 RR2 差异未达显著水平外，与其他品种差异均显著）；有效穗数分别增加 51.49%、13.34%、6.08%、4.28% 和 5.52%（除与 RR2 差异显著之外，与其他再生稻差异均不显著）；结实率分别显著增加 35.24%、27.57%、11.62%、17.55% 和 8.89%，且差异均达显著水平。从产量构成因素看，多年生稻再生季产量较再生稻高的主要原因是再生季单位面积颖花数、有效穗数和结实率均高于再生稻。

目前，对再生稻生育期研究主要围绕留稻桩高度展开。李品汉^[19]、马静^[20]等研究表明，不论是抛秧还是手插，随着留桩高度的增加，有效积温减少，生育期相应缩短。严斧等^[21]的研究指出，留桩 35 cm 的抽穗最早，成熟也最早，抽穗最迟的是留桩 50 cm 的处理。此研究中多年生稻与再生稻均采用低留稻桩 5 cm，对于多年生稻而言，低留桩是可行的，而再生稻还是应留稻桩 25 cm。PR25 再生季全生育期最长，为 110 d，较 RR1、RR2、RR3、RR4、RR5 分别延长 36、20、49、41、45 d，再生稻品种全生育期为 61~90 d，其中，PR25 的营养生长期和营养生长与生殖生长并进期（头季收获至再生季齐穗期）为 75 d，较 RR1、RR2、RR3、RR4、RR5 分别延长 34、23、44、41、44 d，生殖生长期（齐穗后）差异不明显。多年生稻和再生稻品种生育期差异主要在营养生长期，而生殖生长期差异不明显。造成生育期差异的原因是品种间差异，还是由于不同留稻桩高度引起的，有待进一步研究。徐富贤^[8]等研究指出，头季稻齐穗到成熟叶片 SPAD 值衰减指数可作为鉴定再生力的指标。其中 PR25 衰减率最低，为 9.71%，较 RR3、RR1、RR4、RR5 和 RR2 分别减少 48.38%、43.50%、32.68%、28.34% 和 15.86%。灌浆结实期各品种 SPAD 差异不明显，但是后期 SPAD 衰减率多年生稻低于再生稻，说明后期多年生稻叶片早衰程度低于再生稻，剑叶光合持续时间较长。郑景生等^[9]认为再生季稻再生分蘖的生育依赖于头季稻残留的根系，再生季稻穗数及产量与头季稻成熟期和再生季稻齐穗期根系活力呈极显著线性正相关，因此，头季稻成熟期根系伤流量可作为诊断再生力、筛选再生稻品种的重要指标。头季成熟期单株根系伤流量表现为 PR25 > RR2 > RR4 > RR5 > RR1 > RR3，其中 PR25 最大，为 47.9 mg/h，较 RR2、RR4、RR5、RR1 和 RR3 分别增加 5.8%、54.3%、92.2%、124.1% 和 213.3%，多年生稻根系活力在头季成熟期维持在较高水平。此研究中多年生稻与再生稻比较产量等再生指标都表现出优势，主要原因是多年生稻 PR25 头季齐穗后剑叶 SPAD 衰减幅度较小，剑叶具有较强的光合能力，头季成熟期根系维

持在较高活力水平，再生能力较强；再生季多年生稻营养生长期至营养生长与生殖生长并进期明显长于再生稻，进而全生育期较再生稻明显延长，利于干物质积累，从而充分发挥多年生稻产量潜力。PR25 在“一种两收”模式下具有较高的产量潜力。

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不同海拔地区多年生稻稻米品质分析

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摘要: 利用长雄野生稻(*Oryza Longistaminata*) 地下茎无性繁殖特性培育多年生稻已获成功。为明确多年生稻在不同海拔地区种植的稻米品质的差异, 于 2018 年在海拔 550 m(景洪)、955 m(孟连)和 1 250 m(勐海)种植 3 个多年生稻品种(PR23、PR25 和 PR107), 收获后进行稻米品质测定和分析。结果表明, PR23 在景洪和孟连的整精米率符合国家标准优质稻谷 1 级和 2 级, 在勐海的垩白度达到国家标准优质稻谷 3 级, 在景洪、孟连和勐海的直链淀粉含量均符合国家标准优质稻谷 1 级; PR25 在景洪和孟连的整精米率达到国家标准优质稻谷 2 级和 1 级, 在勐海的垩白度达到国家标准优质稻谷 3 级, 在景洪、孟连和勐海的直链淀粉含量均符合国家标准优质稻谷 1 级; PR107 在景洪和孟连的整精米率符合国家标准优质稻谷 2 级和 1 级, 在景洪、孟连和勐海的垩白度符合国家标准优质稻谷 2 级、2 级和 1 级, 在景洪、孟连和勐海的直链淀粉含量均符合国家标准优质稻谷 1 级。

关键词: 多年生稻; 稻米品质; 海拔

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水稻(*Oryza sativa*. L)是全球最重要的粮食作物之一^[1]。但一年生水稻每年均需买种、育秧、移栽、犁田、耙田等生产环节, 种植成本高、劳动强度大, 且长期翻耕犁田导致水土流失严重, 生态环境恶化^[2]。近年来, 人们日益关注土地利用率高、环境友好, 同时有助于提高粮食产量的多年生作物的培育及应用^[3-5]。因此, 部分研究人员提出发展多年生稻, 在水稻生产中实现节本高效、省时省工的同时保护农田环境的设想^[6-7]。多年生稻是指种植一次可以连续收获多年的稻作生产方式, 从第 2 年起水稻生产不再需要买种、育秧、犁田、耙田等环节, 极大地减少了劳动力投入, 降低了劳动强度, 是一项轻简化的稻作生产技术^[8-9]。近年来, 云南大学利用长雄野生稻地下茎无性繁殖特性培育多年生稻获得成功^[8-10], 多年生稻品种 PR23(多年生稻 23)已经通过审定(审定编号: 滇审稻 2018033 号)。最近又培育了多年生稻 PR25(多年生稻 25)和 PR107(云大 107), 这些品种外观品质、蒸煮品质和加工品质较好, 受到广大农民和稻米加工者的喜爱^[10]。然而, 稻米品质受品种遗传特性和环境条件影响较大^[7], 不同海拔地区与稻米品质有密切关系, 其中受气温和土壤肥力影响较大^[11]。例如, 灌浆结实期高温会导致稻米垩白度增加、透明度变差、整精米率下降、蒸煮食味品质变劣等^[12-16]。分析多年生稻在不同海拔地区种植的稻米品质, 对其适宜生产区域划分, 加快生产应用具有重要意义。

1 材料与amp;方法

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1.1 试验材料

本试验以 PR23、PR25 和 PR107 等 3 个多年生稻品种为材料。PR23 和 PR25 系由“RD23/长雄野生稻”杂交组合中选育而来, PR107 系由“滇瑞 449/RD23/长雄野生稻”杂交组合中选育。

1.2 试验设计

试验于 2018 年在云南省 3 个不同海拔地区进行(景洪, 海拔 550 m; 孟连, 海拔 955 m; 勐海, 海拔 1 250 m)。PR23、PR25 和 PR107 分别于 7 月 23 日、7 月 4 日、6 月 28 日播种, 3 叶 1 心期移栽, 各试验田肥力水平一致, 种植面积为 667 m²。田间栽培管理技术均相同: (1) 栽插规格 20 cm×20 cm, 每 hm² 插 0.11 万丛, 每丛 1~2 苗; (2) N:P₂O₅:K₂O=2:1:2, 其中, 氮肥按基肥:分蘖肥:穗肥:粒肥=5:2:2:1 分 4 次施; 磷肥全部基施; 钾肥按基肥:穗肥=1:1 分 2 次施。氮磷钾肥用量及种类: 纯 N 195 kg/hm²、P₂O₅ 97.5 kg/hm²、K₂O 195 kg/hm², 氮肥、磷肥、钾肥分别为尿素(46%)、过磷酸钙(12%)和氯化钾(60%)。 (3) 水分管理参照张琳^[17]的方法, 即“浅水层蘖, 够苗晒田, 有水壮苞, 干湿交替壮籽, 后期晒田活根促苗”。

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表 1 不同海拔地区多年生稻 PR23 稻米品质比较及变异系数

海拔 (m)	加工品质			外观品质			蒸煮品质	
	出糙率(%)	精米率(%)	整精米率(%)	粒长(mm)	垩白度(%)	垩白粒率(%)	直链淀粉含量(%)	胶稠度(mm)
550(景洪)	81.6	73.0	67.7	5.0	8.3	40.0	13.9	75.0
955(孟连)	80.5	73.8	66.9	4.9	12.3	63.0	13.5	70.0
1 250(勐海)	82.0	72.6	35.5	4.8	5.2	34.0	13.2	75.0
均值	81.37	73.13	56.70	4.90	8.60	45.67	13.53	73.33
标准差	0.78	0.61	18.36	0.10	3.56	15.31	0.35	2.89
变异系数(%)	0.95	0.84	32.39	2.04	41.39	33.52	2.59	3.94

表 2 不同海拔地区多年生稻 PR25 稻米品质比较及变异系数

海拔 (m)	加工品质			外观品质			蒸煮品质	
	出糙率(%)	精米率(%)	整精米率(%)	粒长(mm)	垩白度(%)	垩白粒率(%)	直链淀粉含量(%)	胶稠度(mm)
550(景洪)	81.7	74.5	61.0	5.0	8.5	32.0	13.2	73.0
955(孟连)	81.4	72.7	67.6	4.9	10.6	58.0	13.2	70.0
1 250(勐海)	82.3	74.2	40.2	4.8	5.6	40.0	14.5	80.0
均值	81.80	73.80	56.27	4.90	8.23	43.33	13.63	74.33
标准差	0.46	0.96	14.30	0.10	2.51	13.32	0.75	5.13
变异系数(%)	0.56	1.31	25.41	2.04	30.49	30.73	5.51	6.90

1.3 测定项目及方法

成熟时收取适量稻谷置于网袋中晒干,室温储藏3个月后送至农业农村部(武汉)食品质量监督检验测试中心检测,测定稻米加工品质(糙米率、精米率、整精米率)、外观品质(垩白粒率、垩白度、粒长等)和蒸煮品质(直链淀粉含量、胶稠度)等指标。

1.4 数据分析

试验数据采用 Excel 进行统计分析。

2 结果与分析

2.1 不同海拔地区 PR23 稻米品质

从表 1 可见,PR23 的出糙率随海拔升高先降低后增加,在海拔 1 250 m 处(勐海)最高为 82.0%;精米率随海拔升高呈先增加后降低的趋势,在海拔 955 m 处(孟连)最高为 73.8%;整精米率随海拔升高而降低,在海拔 550 m 处(景洪)最高为 67.7%。在海拔 550 m(景洪)至海拔 1 250 m(勐海)范围内,PR23 的出糙率和精米率变异系数较小,说明受海拔高度的影响较小;整精米率变异系数较大,说明其受海拔高度的影响较大。

从表 1 可见,PR23 粒长随海拔升高而下降,但变幅和变异系数均较小,说明受海拔高度影响小;垩白度和垩白粒率随海拔的升高先增加后降低,在海拔 1 250 m 处(勐海)最低,分别为 5.2%和 34.0%;在海拔 550 m(景洪)至海拔 1 250 m(勐海)间,垩白度和垩白粒率变异系数较大,受海拔高度影响大。

从表 1 可见,PR23 直链淀粉含量随海拔升高而降低,在海拔 1 250 m 处(勐海)最低为 13.2%;胶稠度随

海拔升高先降低后升高,在海拔 550 m 处(景洪)和海拔 1 250 m 处(勐海)均为 75.0 mm;在海拔 550 m(景洪)至海拔 1 250 m(勐海)间,PR23 直链淀粉含量和胶稠度变异系数较小,受海拔高度的影响小。

综合来看,PR23 在景洪(海拔 550 m)和孟连(海拔 955 m)的整精米率达到国家标准优质稻谷(GB/T 17891-2017,下简称“国优”)1 级和 2 级,在勐海(1 250 m)的垩白度达到国优 3 级,在三地的直链淀粉含量均符合国优 1 级。

2.2 不同海拔地区 PR25 稻米品质

从表 2 可见,PR25 的出糙率随海拔升高先降低后增加,在海拔 1 250 m 处(勐海)最高,为 82.3%;精米率随海拔升高先降低后增加,在海拔 550 m 处(景洪)最高,为 74.5%;整精米率随海拔升高先增加后降低,在海拔 955 m 处(孟连)最高为 67.6%。在海拔 550 m(景洪)至海拔 1 250 m(勐海)间,PR25 的出糙率和精米率变异系数较小,受海拔高度影响小;整精米率变异系数较大,受海拔高度的影响大。

从表 2 可见,PR25 粒长随海拔升高而下降,且变异系数较小,说明受海拔影响小;垩白度和垩白粒率均随着海拔的升高先增加后降低,分别在海拔 1 250 m(勐海)和海拔 550 m(景洪)较低,平均值分别为 7.05%和 36.00%;但垩白度和垩白粒率在不同海拔地区的变异系数大,受海拔高度影响大。

从表 2 可见,PR25 直链淀粉含量随海拔的升高而增加,在海拔 550 m 处(景洪)和海拔 955 m 处(孟连)较低为 13.20%;胶稠度随海拔的升高先降低后增加,

表 3 不同海拔地区多年生稻 PR107 稻米品质比较及变异系数

海拔 (m)	加工品质			外观品质			蒸煮品质	
	出糙率(%)	精米率(%)	整精米率(%)	粒长(mm)	垩白度(%)	垩白粒率(%)	直链淀粉含量(%)	胶稠度(mm)
550(景洪)	77.5	68.4	55.8	7.6	4.9	15.0	13.8	76.0
955(孟连)	79.3	70.0	56.8	7.3	4.8	28.0	14.9	65.0
1 250(勐海)	77.9	69.3	36.6	7.5	1.0	5.0	13.7	75.0
均值	78.23	69.23	49.73	7.47	3.57	16.00	14.13	72.00
标准差	0.95	0.80	11.38	0.15	2.22	11.53	0.67	6.08
变异系数(%)	1.21	1.16	22.89	2.05	62.34	72.08	4.71	8.45

表 4 多年生稻在不同海拔地区稻米品质表现分级

海拔 (m)	整精米率(%)			垩白度(%)			直链淀粉含量(%)		
	PR23	PR25	PR107	PR23	PR25	PR107	PR23	PR25	PR107
550(景洪)	一级	二级	二级	普通	普通	二级	一级	一级	一级
955(孟连)	二级	一级	一级	普通	普通	二级	一级	一级	一级
1 250(勐海)	普通	普通	普通	三级	三级	一级	一级	一级	一级

在海拔 550 m 处(景洪)和 1 250 m 处(勐海)较高;在海拔 550 m(景洪)至海拔 1 250 m(勐海)区域间,直链淀粉含量和胶稠度变异系数较小,说明蒸煮品质受海拔高度影响较小。

综合来看,在海拔 550 m 至海拔 1 250 m 之间,PR25 在景洪(550 m)和孟连(955 m)整精米率符合国优 2 级和 1 级,在勐海(1 250 m)垩白度符合国优 3 级,在三地的直链淀粉含量均符合国优 1 级。

2.3 不同海拔地区 PR107 稻米品质

从表 3 可见,PR107 的出糙率、精米率和整精米率均随海拔升高先增加后降低,在海拔 955 m 处(孟连)最高,分别为 79.3%、70.0%和 56.8%;在海拔 550 m(景洪)至海拔 1 250 m(勐海)间,PR107 出糙率和精米率的变异系数较小,整精米率变异系数较大,说明出糙率和精米率受海拔影响较小,而整精米率受海拔高度影响较大。

从表 3 可见,PR107 粒长随海拔升高先降低后增加,且其变化幅度和变异系数较小,说明 PR107 粒长受海拔高度影响较小;随海拔的升高 PR107 垩白度和垩白粒率先增加后降低,在海拔 1 250 m 处(勐海)最低分别为 1.00%和 5.00%;垩白度和垩白粒率变异系数较大,说明外观品质不稳定,受海拔高度影响较大。

从表 3 可见,PR107 直链淀粉含量随海拔的升高先增加后下降,在海拔 1 250 m 处(勐海)最低为 13.7%;胶稠度随海拔的升高先降低后增加,在海拔 550 m 处(景洪)和 1 250 m 处(勐海)较高。

综合来看,PR107 稻米加工品质和蒸煮品质表现较为稳定,外观品质在海拔 1 250 m 处(勐海)表现较优。PR107 在景洪(550 m)和孟连(955 m)的整精米率符合国优 2 级和 1 级,在景洪(550 m)、孟连(955 m)和

勐海(1 250 m)的垩白度符合国优 2 级、2 级和 1 级,直链淀粉含量均符合国优 1 级。

3 讨论与结论

不同海拔差异是影响稻米品质的重要因素之一。在加工(碾磨)品质方面,前人研究表明,稻米的出糙率和精米率受海拔高度影响较小^[18-19],而整精米率受海拔影响较大,随海拔升高,整精米率明显增加^[19-20]。这与本研究结果一致。本研究表明,在海拔 550~1 250 m 区域,多年生稻稻米的出糙率和精米率受海拔影响较小,但不同海拔区域对整精米率影响较大,在海拔 550~955 m 的低海拔地区,整精米率较高,均达到了国优 2 级以上(表 4),说明在低海拔地区(550 ~955 m)种植多年生稻其稻米加工品质更优。

在外观品质方面,前人研究表明,海拔高度对稻米垩白的影响较大,随海拔升高垩白粒率明显下降^[18,21-22]。本研究表明,在海拔 550~1 250 m 区域,随海拔升高多年生稻稻米垩白度和垩白粒率呈先增加后降低的趋势。这与张现伟等^[23]的研究结果一致。本研究中,不同海拔区域多年生稻稻米垩白度和垩白粒率变异系数较大,说明多年生稻外观品质受海拔高度影响大,但在中海拔 1 250 m 区域多年生稻稻米垩白度达到了国优 3 级以上(表 4)。说明多年生稻在此区域种植外观品质更优。

在蒸煮(食味)品质方面,苏振喜等^[19]认为,直链淀粉含量受海拔的影响较小,其差异主要来自品种间的差异,而海拔梯度对胶稠度的影响较大。黄宗洪等^[24]研究表明,杂交稻两优 363 的直链淀粉含量有随海拔升高而增加的趋势。本研究结果与苏振喜等^[19]研究结果一致,不同海拔区域(550~1 250 m)对多年生稻稻米直

链淀粉含量影响较小;胶稠度随海拔的升高先降低后增加,但不同海拔区域胶稠度的变异系数较小。结果表明,多年生稻稻米的蒸煮品质表现较为稳定,且直链淀粉含量在参试区域均达到国优1级(表4)。

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Quality Analysis of Perennial Rice in Different Altitude Regions

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Abstract: Perennial rice which is breeding by the clonal propagation characteristic via rhizome of *Oryza longistaminata* has been successful. In order to clarify the differences in perennial rice quality at different altitudes, 3 perennial rice varieties PR23, PR25 and PR107 were applied at 3 different altitudes of 550 m (Jinghong), 955 m (Menglian) and 1 250 m (Menghai) in 2018. The results showed that the head rice rate of PR23 in Jinghong and Menglian reached the first and second grade of national standard for high quality rice, respectively. But it's chalkiness degree in Menghai reached the third grade of national standard for high quality rice, and the amylose content in Jinghong, Menglian and Menghai met the first grade of national standard for high quality rice. The head rice rate of PR25 in Jinghong and Menglian reached the second and first grade of national standard for high-quality rice, respectively. It's chalkiness degree in Menghai reached the third grade of national standard for high quality rice, respectively, the amylose content in Jinghong, Menglian and Menghai met the first grade of national standard for high quality rice. The head rice rate of PR107 in Jinghong and Menglian reached the second and first grade of national standard for high quality rice, respectively. It's chalkiness degree in Jinghong, Menglian and Menghai met the second, second and first grade of national standard for high quality rice, respectively, and the amylose content in Jinghong, Menglian and Menghai met the first grade of national standard for high quality rice.

Key words: perennial rice; rice quality; altitude

多年生稻云大 107 产量潜力分析

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摘要:利用长雄野生稻地下茎无性繁殖特性培育具有多年生性的栽培稻品种已经获得成功。云大 107 是通过“滇瑞 449/RD23/长雄野生稻”杂交选育出来的具有多年生性的优质稻品种。为明确云大 107 的产量潜力,进而为优化其栽培技术提供科学依据,笔者用云南主栽的优质稻品种滇屯 502、滇瑞 449、文稻 5 作对照,于 2018 年在云南景洪进行田间试验,调查分析了各品种生育期、干物质积累、光合特性、产量及产量潜力等性状。结果表明,云大 107 产量可达 564.52 kg/667 m²,较滇屯 502、文稻 5 和滇瑞 449 分别增产 25.94%、5.41%和 2.93%,其中与滇屯 502 相比差异达显著;从产量构成看,云大 107 每穗粒数、千粒重均比对照文稻 5、滇屯 502 和滇瑞 449 高,粒多粒大是其高产的原因;同时,云大 107 剑叶净光合速率分别比滇屯 502、滇瑞 449 和文稻 5 增加 4.45%、4.65%和 16.83%,差异显著。因此,挖掘云大 107 产量潜力的主要途径是提高其每穗粒数,同时提高齐穗后剑叶光合能力,以积累较多光合产物,进而提高成熟期生物产量。

关键词:多年生稻;干物质;光合特性;产量;产量潜力

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近年来,云南大学利用长雄野生稻地下茎无性繁殖特性培育的多年生稻获得了成功^[1-3],多年生稻品种多年生稻 23 已经通过了云南省审定(审定编号:滇审稻 2018033 号)。多年生稻是指种植一次就可以连续收获多年的稻作生产方式,从第 2 年起水稻生产不再需要种子、育秧、犁田耙田、栽秧等环节,不仅减少了劳动力投入和生产成本,也大大降低了劳动强度,是一项轻简化的稻作生产技术。最近,云南农业大学又从“滇瑞 449/RD23/长雄野生稻”杂交组合中选育出了具有多年生性的优质稻品种云大 107。为了明确云大 107 的产量潜力,为其栽培技术优化提供依据,我们用云南主栽的优质稻品种滇屯 502、滇瑞 449、文稻 5 作对照,于 2018 年在云南景洪进行了田间比较试验,以期云大 107 的推广与栽培技术的优化提供详实数据和理论依据。

1 材料与与方法

1.1 供试材料与供试地点

供试材料为滇屯 502、文稻 5、滇瑞 449、云大 107。试验于 2018 年在云南景洪市嘎洒镇试验基地进行(海拔 550 m)。试验地土壤基础肥力:pH 值 5.05,有机质含量 34.0 g/kg,全氮 2.1 g/kg,碱解氮 155.60 mg/kg,速效磷 7.58 mg/kg,速效钾 139.10 mg/kg。

1.2 试验设计

采用随机区组设计,3 次重复,小区面积 20 m² (长×宽=4 m×5 m)。种植方式和施肥措施与当地生产水平类似。7 月 23 日播种,8 月 17 日移栽,移栽行株距 20 cm×20 cm,每 667 m² 插 1.67 万丛,每丛 1~2 苗;氮肥、磷肥、钾肥分别选用尿素(46%)、过磷酸钙(12%)和氯化钾(60%),纯 N 用量 13 kg/667 m²,P₂O₅ 6.5 kg/667 m²,K₂O 13 kg/667 m²。其中,氮肥按基肥:分蘖肥:穗肥:粒肥=5:2:2:1 分 4 次施,磷肥全部作基肥,钾肥按基肥:穗肥=1:1 分 2 次施。水分管理和病虫害防治参照水稻高产管理措施进行。

1.3 测定项目及方法

1.3.1 生育期

记载播种期、成熟期,并计算最终的全生期天数。

1.3.2 干物质积累

分别在齐穗期和成熟期取样,每小区取 5 丛,洗净泥沙,测定茎蘖数,然后剪去根。齐穗期将样品分成茎、叶、穗 3 部分;成熟期将样品分成稻草、枝梗、实粒、秕粒 4 部分。样品整理好及时放入烘箱 105℃杀青 30 min,后调温度至 75℃烘干至恒质量,分别测定干物质

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表 1 不同品种产量及产量构成表现

品种	有效穗数 (万/667 m ²)	每穗粒数 (粒)	结实率 (%)	千粒重 (g)	理论产量 (kg/667 m ²)	实际产量 (kg/667 m ²)
滇屯 502	17.23 ab	127.96 b	78.03 a	29.32 a	500.73 a	448.25 b
文稻 5	18.89 ab	120.88 b	83.80 a	29.69 a	566.72 a	535.57 a
滇瑞 449	22.78 a	120.07 b	82.35 a	25.23 b	569.34 a	548.46 a
云大 107	16.23 b	138.82 a	82.38 a	30.80 a	570.59 a	564.52 a

同列数据后不同小写字母表示各品种间差异在 0.05 水平显著。下同。

表 2 不同品种生育期表现

品种名称	始穗期 (月-日)	移栽期 (月-日)	齐穗期 (月-日)	成熟期 (月-日)	播始历期 (d)	始穗-成熟 (d)	全生育期 (d)
滇屯 502	10-22	08-17	10-30	12-03	91	42	133
文稻 5	10-04	08-17	10-13	11-18	73	45	118
滇瑞 449	10-25	08-17	11-03	12-06	94	42	136
云大 107	10-20	08-17	10-26	11-29	89	40	129

量。

1.3.3 净光合速率和叶绿素含量

在齐穗期, 用 LI-6400XT 便携式光合测定仪梭形叶室测定剑叶净光合速率(Pn), 每个小区测 3 株, 测定时间选择晴朗天气的上午 9:00—11:00; 同时将测定净光合速率(Pn) 剑叶对应做好标记取样放入封口袋中, 带回实验室测其叶绿素含量。叶绿素含量的测定参考张其德^[4]的方法。每次测定重复 3 次, 取平均值。

1.3.4 产量与产量构成

采用 5 点取样法进行取样调查, 调查有效穗数、穗粒数、结实率、千粒重等性状, 计算理论产量。同时每个小区取 5 m² 进行实割测产, 计算实际产量。

1.4 数据分析

试验数据采用 Excel 和 SPSS 23.0 软件进行处理和分析。

2 结果与分析

2.1 产量及产量构成

从表 1 可见, 实际产量和理论产量均表现为云大 107>滇瑞 449>文稻 5>滇屯 502, 其中实际产量云大 107 为 564.52 kg/667 m², 较滇屯 502、文稻 5 和滇瑞 449 分别增加 25.94%、5.41%和 2.93%, 与滇屯 502 相比产量差异显著。从产量构成因素看, 云大 107 每穗粒数为 138.82 粒, 显著多于滇瑞 449、文稻 5 和滇屯 502, 分别提高 8.49%、14.84%和 15.62%; 云大 107 有效穗数 16.23 万/667 m², 较滇屯 502、文稻 5 和云大 107 分别减少 5.80%、14.08%和 28.75%, 其中与滇瑞 449 差异显著; 云大 107 千粒重 30.8 g, 显著高于滇瑞 449; 各品种之间结实率差异不显著。可见, 云大 107 的产量比云南

主栽优质稻品种略高, 其高产的原因主要在于有较多的穗粒数和较高的千粒重。

2.2 生育期

从表 2 可见, 全生育期表现为滇瑞 449>滇屯 502>云大 107>文稻 5, 云大 107 较亲本滇瑞 449 缩短 7 d, 较滇屯 502 缩短 4 d, 比文稻 5 长 11 d。品种间生育期差异主要表现在播始历期, 为 3~21 d, 而始穗至成熟期差异不明显。说明云大 107 的生育期适合云南优质稻生产的生育期需求。

2.3 干物质积累

从表 3 可见, 云大 107 成熟期干物质质量为 1 984.8 g/m², 比文稻 5、滇屯 502、滇瑞 449 分别增加 28.87%、19.94%、11.44%, 其中与文稻 5 差异显著; 齐穗期干物质质量为 1 305.4 g/m², 比滇瑞 449 显著增加 308.7 g/m², 而与滇屯 502、文稻 5 差异不显著; 云大 107 收获指数为 0.55, 与滇瑞 449、滇屯 502 以及文稻 5 差异不显著; 云大 107 齐穗至成熟期生长速率为 20.0 g/(m²·d), 显著高于滇屯 502 和文稻 5。这 4 个参试品种的产量与成熟期干物质质量和生长速率呈显著正相关 (r=0.775*, r=0.778*)(表 4)。总的来看, 云大 107 在成熟期及齐穗期的干物质质量均大于其他优质稻品种, 收获指数和生长速率亦较高, 具有适应云南优质稻区种植的潜力。

2.4 光合特性

2.4.1 叶绿素含量

从图 1 可见, 云大 107 的叶绿素 a、类胡萝卜素和叶绿素 a+b 小于滇屯 502, 但均大于文稻 5 和滇瑞 449。表明云大 107 在云南优质稻主栽区具有较高的光合特性, 利于通过优化栽培措施提高产量。

2.4.2 净光合速率

表 3 不同品种干物质积累、生长速率、收获指数差异

品种	齐穗期干物质质量 (g/m ²)	成熟期干物质质量 (g/m ²)	齐穗期-成熟期生长速率 [g/(m ² ·d)]	收获指数 (%)
滇屯 502	1 331.6 a	1 654.8 ab	9.8 c	0.48 a
文稻 5	1 063.3 bc	1 540.1 b	13.2 bc	0.59 a
滇瑞 449	996.7 c	1 781.0 ab	23.8 a	0.51 b
云大 107	1 305.4 ab	1 984.8 a	20.0 ab	0.55 ab

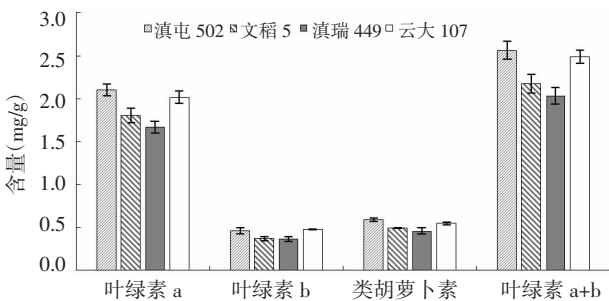
表 4 不同品种干物质积累、生长速率、收获指数相关性分析

项目	齐穗期干物质质量	成熟期干物质质量	齐穗-成熟期生长速率	收获指数	产量
齐穗期干物质质量	1				
成熟期干物质质量	0.403	1			
生长速率	-0.360	0.706*	1		
收获指数	-0.195	-0.103	-0.005	1	
产量	-0.041	0.601*	0.615*	0.464	1

*表示在 P<0.05 条件下相关性显著,**表示在 P<0.01 条件下相关性显著。下同。

表 5 不同品种净光合速率比较

品种	净光合速率 [$\mu\text{mol}/(\text{m}^2\cdot\text{s})$]	气孔导度 [$\text{mol}/(\text{m}^2\cdot\text{s})$]	胞间 CO ₂ 浓度 ($\mu\text{mol}/\text{mol}$)	蒸腾速率 [$\mu\text{mol}/(\text{m}^2\cdot\text{s})$]
滇屯 502	25.19 b	0.52 b	261.97 ab	8.73 a
文稻 5	22.52 c	0.50 ab	267.39 ab	8.16 b
滇瑞 449	25.14 b	0.48 b	252.24 c	7.92 b
云大 107	26.31 a	0.61 a	275.11 a	4.86 c


图 1 云南主栽优质稻不同品种叶绿素含量差异

从表 5 可见,云大 107 齐穗期剑叶净光合速率为 26.31 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$,显著高于滇屯 502、滇瑞 449 和文稻 5,分别增加 4.45%、4.65%和 16.83%;而气孔导度是 0.61 $\text{mol}/(\text{m}^2\cdot\text{s})$,显著高于滇屯 502、滇瑞 449,与文稻 5 持平;胞间 CO₂ 浓度为 275.11 $\mu\text{mol}/\text{mol}$,和文稻 5、滇屯 502 以及滇瑞 449 持平;蒸腾速率 4.86 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$,显著小于文稻 5、滇屯 502 和滇瑞 449。云大 107 的净光合速率与叶绿素 a、叶绿素 b、叶绿素 a+b 和类胡萝卜素呈极显著正相关性(相关系数分别为 0.880**、0.906**、0.908**、0.895**) (表 6)。从光合特性和净光合速率可以看出,云大 107 具有高产的光合潜力。

3 讨论与结论

3.1 产量与产量构成关系

在产量构成要素中,有效穗数、每穗实粒数是衡量库容量大小的主要指标,千粒重反应的则是库容的充实程度。研究表明,在高产水平下产量构成要素中,千粒重与产量的偏相关系数最大,每穗实粒数次之^[5],所以说提高库容量是获得高产的重要途径,而库的充实程度是获得高产的保证。研究证明,增加穗粒数和千粒重是获得高产的直接原因,尤其在高产条件下关系更为密切^[6]。本研究中,实际产量和理论产量均表现为云大 107>滇瑞 449>文稻 5>滇屯 502,云大 107 的每穗粒数显著多于滇屯 502、文稻 5 和滇瑞 449,而千粒重也高于滇屯 502、文稻 5 和滇瑞 449。与其他品种相比,云大 107 产量潜力优势主要体现在穗大、粒重上,通过调控栽培措施可以进一步协调产量构成四要素的关系,进而挖掘云大 107 产量潜力。

3.2 产量与干物质积累、收获指数关系

水稻各器官干物质的积累是产量形成的基础^[7]。产量潜力提高更多地是依靠增加生物产量和协调生物产量与收获指数的关系^[8]。高产高效栽培和超高产栽培可以显著提高水稻干物质总积累量,特别是齐穗至成熟阶段的干物质积累量,使产量随干物质的增加而同步增加^[9]。云大 107 成熟期的干物质积累量最大,这也是云大 107 产量高于其他优质稻的主要原因之一。

3.3 剑叶净光合速率、叶绿素含量与产量、干物质积

表 6 不同品种剑叶净光合速率和叶绿素含量的相关性分析

项目	叶绿素 a	叶绿素 b	类胡萝卜素	叶绿素 a+b	净光合速率
叶绿素 a	1				
叶绿素 b	0.896**	1			
类胡萝卜素	0.945**	0.870**	1		
叶绿素 a+b	0.994**	0.937**	0.942**	1	
净光合速率	0.774**	0.820**	0.825**	0.801**	1

累的关系

产量变化主要取决于抽穗至成熟期光合生产能力^[10], 而光合生产能力又主要取决于净光合速率和蒸腾速率的快慢。云大 107 净光合速率显著高于滇屯 502、滇瑞 449 和文稻 5, 气孔导度和胞间 CO₂ 浓度显著大于或略高于其他 3 个云南主栽的优质稻; 蒸腾速率却显著小于文稻 5、滇屯 502 和滇瑞 449。可见, 云大 107 具有较高的光合潜力, 这也是其产量高于其他优质稻品种的主要原因之一。

光合生产能力取决于植物体叶片的叶色, 水稻叶色的深浅是由体内叶绿素含量的多寡决定的, 叶绿素在光合作用的光能吸收、传递和转换中起着关键作用^[11]。叶绿素含量与净光合速率呈显著相关性, 并且直接影响产量^[12], 叶绿素含量高, 有助于获取更多太阳辐射量, 也利于光合产物的形成和积累, 提高植物的光能利用率。本研究表明, 净光合速率与叶绿素 a、叶绿素 b、叶绿素 a+b 和类胡萝卜素呈极显著正相关性, 云大 107 除了叶绿素 a、类胡萝卜素和叶绿素 a+b 小于滇屯 502 外, 其他各指标均大于文稻 5 和滇瑞 449。

云大 107 较云南主栽其他优质稻产量高的主要原因是粒多粒大, 同时生长后期具有较高的光合产物生产能力, 保证成熟期有较高干物质积累。因此, 提高包括多年生稻云大 107 在内的云南优质稻产量及挖掘产量潜力的主要途径是提高每穗粒数, 同时提高齐穗后剑叶光合能力, 以积累较多光合产物, 进而提高成熟期生物产量。

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Yield Potential Analysis of Perennial Rice Yunda 107

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Abstract: Perennial rice has been successfully bred by the clonal propagation characteristic via rhizome of *Oryza longistaminata*, can survive for many years. Yunda 107 is a perennial rice variety with high quality, selected through the cross of ‘Dianrui449//RD23//Oryza longistaminata’. In order to explore the yield potential of Yunda 107, an experiment was conducted in 2018 using high quality rice varieties Diantun 502, Dianrui 449 and Wendao 5 as controls. In the experiment, we investigated the traits such as growth period,

dry matter accumulation, photosynthetic characteristics, yield and yield potential of each tested variety. The results showed that, the yield of Yunda 107 can reach 564.52 kg/667 m², which increase by 25.94%, 5.41% and 2.93% compared with Diantun 502, Wendao 5 and Dianrui 449, respectively, and the difference is significant compared with Diantun 502. In terms of yield composition, the number of grains per panicle and the weight per thousand grains of Yunda 107 were higher than those of Wendao 5, Diantun 502 and Dianrui 449. The large number and size of grains were the main reason for its higher yield. At the same time, the net photosynthetic rate of flag leaves of Yunda 107 increased by 4.45%, 4.65% and 16.83%, compared with Diantun 502, Dianrui 449 and Wendao 5, respectively, with significant differences. Therefore, the main way to tap the yield potential of Yunda 107 is to increase the number of grains per panicle and the photosynthetic capacity of flag leaves after full heading, so as to accumulate more photosynthetic products, thereby increasing the biological yield at mature stage.

Key words: perennial rice; dry matter; photosynthetic characteristics; yield; yield potential.

·综合信息·

至 2020 年农业农村部认定的 133 个超级稻品种

2020 年 6 月 8 日, 农业农村部认定 11 个超级稻品种, 退出 10 个超级稻品种冠名, 至此农业农村部共认定(不含退出) 133 个超级稻品种, 具体列于表 1。另附认定而退出冠名的超级稻品种。

表 1 至 2020 年农业农村部认定的 133 个超级稻品种

类型	品种名称	认定年份	育种单位	类型	品种名称	认定年份	育种单位
粳型 常规 稻 (26)	吉粳 88	2005	吉林省农科院水稻所	籼型 三系 杂交 稻 (49)	中浙优 1 号	2005	中国水稻研究所
	桂农占	2006	广东省农科院水稻所		II 优明 86	2005	福建省三明市农科所
	龙粳 21	2009	黑龙江省农科院水稻研究所		II 优 602	2005	四川省农科院水稻所
	辽星 1 号	2007	辽宁省农科院稻作所		天优 998	2005	广东省农科院水稻所
	楚粳 27	2007	云南省楚雄州农科所		Q 优 6 号	2006	重庆中一种业有限公司
	沈农 9816	2011	沈阳农业大学		珞优 8 号	2009	武汉大学生科院
	连粳 7 号	2012	连云港市农业科学研究院		五优 308	2010	广东省农业科学院水稻研究所
	龙粳 31 号	2013	黑龙江省农业科学院佳木斯水稻研究所等		五丰优 T025	2010	江西农业大学
	松粳 15 号	2013	黑龙江省农业科学院五常水稻研究所		天优 3301	2010	福建省农业科学院生物技术研究所等
	镇稻 11 号	2013	江苏丘陵地区镇江农业科学研究所		特优 582	2011	广西农业科学院水稻研究所
	扬粳 4227	2013	江苏里下河地区农业科学研究所		德香 4103	2012	四川省农业科学院水稻高粱研究所
	宁粳 4 号	2013	南京农业大学农学院		天优华占	2012	中国水稻研究所等
	龙粳 39	2014	黑龙江省农业科学院佳木斯水稻研究所等		宜优 673	2012	福建省农科院水稻所
	莲稻 1 号	2014	佳木斯市莲梗种业公司等		深优 9516	2012	清华大学深圳研究生院
	长白 25 号	2014	吉林省农业科学院水稻研究所		天优 3618	2013	广东省农业科学院水稻研究所
	南粳 5055	2014	江苏省农业科学院粮食作物研究所		天优华占	2013	中国水稻研究所等
	武运粳 27 号	2014	江苏(武进)水稻研究所等		中 9 优 8012	2013	中国水稻研究所
	扬育粳 2 号	2015	江苏盐城市盐都区农业科学研究所		H 优 518	2013	湖南农业大学等
	南粳 9108	2015	江苏省农业科学院粮食作物研究所		五丰优 615	2014	广东省农业科学院水稻研究所
	镇稻 18 号	2015	江苏丰源种业有限公司等		盛泰优 722	2014	湖南洞庭高科种业股份有限公司等
	吉粳 511	2016	吉林省农业科学院水稻所		内 5 优 8015	2014	中国水稻研究所
	南粳 52	2016	江苏省优质水稻工程技术研究中心等		荣优 225	2014	江西省农业科学院水稻研究所等
	南粳 0212	2017	江苏省农业科学院粮食作物研究所等		F 优 498	2014	四川农业大学水稻研究所等
	楚粳 37 号	2017	楚雄州农业科学研究所推广所		宜香优 2115	2015	四川省绿丹种业有限责任公司等
	宁粳 7 号	2018	南京农业大学		深优 1029	2015	江西现代种业股份有限公司
	苏垦 118	2020	江苏省农业科学院粮食作物研究所		德优 4727	2016	四川省农业科学院水稻高粱研究所
籼型 常规 稻 (8)	玉香油占	2007	广东省农科院水稻所	丰田优 553	2016	广西农业科学院水稻研究所	
	中嘉早 17	2010	中国水稻研究所等	五优 662	2016	江西惠农种业有限公司等	
	合美占	2010	广东省农业科学院水稻研究所	吉优 225	2016	江西省农业科学院水稻研究所等	
	中早 35	2012	中国水稻研究所	五丰优 286	2016	江西现代种业股份有限公司	
	金农丝苗	2012	广东省农科院水稻所	五优航 1573	2016	江西省超级水稻研究发展中心等	
	中早 39	2013	中国水稻研究所	宜香 4245	2017	宜宾市农业科学院	
	华航 31 号	2015	华南农业大学植物航天育种研究中心	吉丰优 1002	2017	广东省农业科学院水稻研究所等	
	中组 143	2020	中国水稻研究所	五优 116	2017	广东省现代农业集团有限公司等	

(下转第 66 页)

水稻叶面积指数与产量关系研究进展

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摘要:叶片作为水稻器官建成的物质基础,与水稻群体中光环境的优劣和光能利用率的高低关系密切。而叶面积指数(LAI)的大小直接与水稻最终产量相关,且水稻冠层中光合有效辐射吸收系数与叶面积指数相关性极显著。文章综述了水稻在生长的各个阶段叶面积指数和产量之间的关系,同时通过优化品种、改善栽培措施等手段增加水稻最适叶面积指数,提高水稻产量,以期为高产水稻适宜叶面积指数的预测及合理冠层结构的调控提供理论依据。

关键词:杂交水稻;叶面积指数;最适叶面积指数;水稻生育时期;产量

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The Relationship Between Leaf Area Index and Yield of Rice: Research Progress

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Abstract: Leaf, as the material basis for constructing the rice organs, is closely related to the quality of the light environment and the utilization rate of light energy. The leaf area index (LAI) is an important indicator related to rice yield, and is significantly correlated with the light and effective radiation absorption coefficient in rice canopy. In this paper, we reviewed the relationship between the LAI in different growth periods of rice and the yield, and pointed out that the optimal LAI could be increased based on variety selection and cultivation measures, to achieve the high yield. The study could provide a theoretical basis for developing a predicting system of the optimal LAI and for regulating the rational canopy structure of rice.

Keywords: hybrid rice; leaf area index; optimum leaf area index; rice growth period; yield

0 引言

大米养活了世界上约一半以上的人口,而水稻作为重要的粮食作物,其产量高低在影响人们日常生活对食物需求的同时也关系着国家粮食安全^[1-2]。根据国际稻米研究所的数据,2025年我们将需要8亿t大米^[3]。中国作为世界上最早栽培水稻的国家之一,在长期栽培中,培育出了许多优良品种并形成了独具特色的稻作技术。杂交水稻的诞生为世界的粮食安全和平稳发展做出了重大贡献^[4],然而杂交水稻的发展受到诸多因素的制约。提高作物产量可从改良株型和杂种优势利用两方面进行。在水稻成熟的整个过程,实

际上就是干物质的累计和分配的过程,高的生物产量是实现高产的关键^[5]。杨胜荣等^[6]相关研究表明,可通过提高生物产量(如增加茎蘖数量,提高叶面积系数,提高光合效率等)来选育杂交水稻新组合,从而达到高产的目的^[7]。可见,将二者结合将会是培育杂交水稻的最佳途径。叶片作为水稻器官建成的物质基础,将会直接影响到水稻对于光能的利用有效性。叶片中光合作用量占据整个植株光合作用量的90%,是栽培、育种等过程中的重要指标,同时也是在水稻栽培的过程中管理、病虫害预防等的重要参考标准^[8]。由于各叶位叶片出生、死亡的时间及着生部位不同,对器官生长

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所起的作用也各不相同^[9]。徐富贤等^[10]研究表明,杂交中稻各叶位叶片对头季稻和再生稻产量形成作用的趋势是一致的,即倒1叶>倒2叶>倒3叶>倒4叶及以下叶,但其作用程度不同。所谓的叶面积指数指的是在1 m²土地面积上植物叶片的总面积和土地面积的比值,也称叶面积系数。它主要是对植物表面物质和能量之间转换、植物生长情况、植物产量的一个重要指标,同时也是栽培措施的一个重要参考指标^[11],在植物遥感、气候模型等多个方面的研究中起到重要作用^[12-13]。合适的叶面积指数为植物各个器官资源的平衡奠定了基础^[14-20],其大小影响光合速率的高低即决定了产量的高低,因此水稻等高产类植株一定要有一个合适的最大叶面积指数^[21-25]。在本次研究中,通过对水稻叶面积指数和产量之间的关系进行阐述,为高产水稻适宜叶面积指数的预测以及合理株型、冠层结构的调控等提供理论依据,最终为水稻产量的提高提供合理的数据支撑及栽培技术支持。

1 分蘖期水稻叶面积指数与产量的关系

莫家让^[26]指出,在水稻生育期中群体结构比较合适的叶面积指数分蘖期为3左右,杂交水稻在分蘖盛期以后的叶面积指数常常高于一般品种;潘圣刚等^[27]研究结果表明超高产栽培水稻叶面积指数分蘖盛期为3.0~3.5左右,费聪等^[28]相关研究结果表明‘甬优538’、‘秀水134’分蘖期最适叶面积指数分别在6左右和5左右,与产量显著相关。张林青^[29]研究结果显示,分蘖期叶面积指数适宜值与叶片数量多少有关,合理的分蘖临界叶龄期的叶面积指数适宜值为1.8~2.2,4叶以上叶面积指数适宜值为1.6~1.8,同时表明大于等于3叶的茎蘖叶面积指数在总叶面积指数的占比直接决定分蘖临界叶龄期叶面积指数的大小。朱秋明等^[30]研究结果表明分蘖期叶面积指数与水稻单位面积的总穗数、穗粒数均呈正相关关系,和千粒的质量和结实率都呈现出负相关的关系;而胡磊等^[31]研究表明叶面积指数与早稻穗粒数和千粒质量均无相关性,其可能是千粒质量和穗粒数是早稻品种本身的遗传特性。以上研究表明,不同品种的杂交稻在分蘖期最佳的叶面积指数不同,同时与叶片数量多少和品种本身特性等有关,但最终结果都表明叶面积指数和产量都表现出二次方程关系。在水稻分蘖期提高最适叶面积指数对提高产量具有重要作用。

2 拔节期水稻叶面积指数与产量的关系

张巍巍等^[32]研究结果表明:水稻处于拔节时期最合适的叶面积指数——‘牡丹江32’在5.0左右,‘牡响1号’在11.0左右。费聪等研究表明‘甬优538’、‘秀水

134’等在拔节的时候,最适当的叶面积指数均在8左右。张林青等^[33]研究结果表明在拔节的时候,最适当的叶面积指数的大小主要取决于4叶及其以上茎蘖数,为3.9~4.2。拔节期,最适当的叶面积指数随4叶及其以上茎蘖数的增多而增大,但只有茎蘖数最适宜时,叶面积指数才能达到最大值,其叶面积指数的适宜值为3.5~3.8。在朱秋明等研究中,在水稻拔节期,叶面积指数和单位面积总穗数、穗粒数呈现出正关联,和千粒质量与结实率之间表现出负关联,同分蘖期相似。

分蘖期与拔节期是水稻生长过程中的第一个阶段,和抽穗期间的叶面积指数大小密切相关。但高产不仅与适宜的叶面积指数相关,还与叶面积组成相关,因此开展生育前期叶面积指数组成的研究对产量的提高有一定的指导意义。同时,在实际水稻栽培生产中,充分发挥并利用4叶以上大分蘖的优势,可以提高水稻群体质量,保证产量。

3 孕穗期水稻叶面积指数与产量的关系

孕穗期是水稻营养生长和生殖生长并进的时期,在根、茎、叶继续生长的同时进行穗的分化和形成,是决定穗大、粒多的关键时期,直接影响产量的形成。孕穗期,水稻叶面积指数同样也呈现出上升的趋势,当水稻的叶面积指数增大的时候,水稻面积的总穗数、穗粒数也随着提高,千粒质量、结实率都呈现出降低的趋势。随着生育期的推进,虽有部分叶片衰落,但可通过栽培技术措施来调节最适叶面积指数,从而保持水稻高产^[34]。费聪等研究中,孕穗期‘甬优538’最适叶面积指数在10左右,‘秀水134’在12左右。莫家让指出,孕穗至抽穗期叶面积指数达最大值5.5~7.5。由此可见,在孕穗期有适宜的最大叶面积指数,协调好水稻叶片营养物质的转运及分配,对提高产量至关重要。

4 抽穗开花期水稻叶面积指数与产量的关系

有研究表明开花期水稻叶面积指数达到最大值,水稻进入生殖生长旺季。此时,叶面积指数与水稻单位面积的总穗数、穗粒数整体呈正相关的关系。抽穗期的叶面积指数与抽穗前的群体物质生产呈极显著相关^[35-36]。朱雪兰^[37]研究表明叶面积指数的最大值与测定时期有关,总体上呈现出生育前期不断增加,抽穗期达到峰值,生育后期不断减小的趋势^[38];薛亚峰等^[39]研究结果表明在水稻抽穗的时候,叶面积指数和产量彼此间呈现出二次方程关系,且相关性达显著水平,说明可通过将冠层中叶面积指数的合理分配设计为顶部第二叶最大,其次是第三和第四叶来使水稻获得高产^[40]。

5 灌浆期水稻叶面积指数与产量的关系

研究表明:灌浆期,对于‘牡丹江32’来说,最佳叶面积指数是4.0左右,‘牡响1号’在6.0左右;‘甬优538’在7左右,‘秀水134’在8左右。不同品种的水稻灌浆期最适叶面积指数不同,可根据品种特性调节叶面积指数,增大光合效率,提高生物产量积累量从而提高经济产量,但灌浆期最适叶面积指数不宜过大。

6 成熟期水稻叶面积指数与产量的关系

研究表明:‘牡丹江32’成熟期最佳的叶面积指数在6.0上下浮动,‘牡响1号’在7.0左右。乳熟期稻穗的同化产物迅速积累,是籽粒形成的关键时期,当叶面积指数越大,单位面积的总穗数也就越大,结实率和千粒质量越小。水稻在成熟期的时候,叶面积指数增大将会促进水稻产量的提高,可是因为在这一时期整体干物质质量会受到叶片光合面积的影响,另外因为转运物质的影响,在成熟时期水稻的产量和叶面积指数的相关系数是较小的。朱德峰等研究表明叶面积指数决定了成熟期的干物质产量,同时也决定了冠层光合的强度。

7 总结

FACE条件下,叶面积指数是一个连续变化的过程,符合水稻生长发育进程,在抽穗之前,水稻在生长过程中,水稻群体的叶面积指数逐渐增大,在孕穗到抽穗期达到峰值,水稻抽穗之后叶片会逐渐的成熟至衰老,此时叶面积指数会逐渐的降低,表现出单峰的曲线^[41-42]。而上述数据表明,水稻生育前期的产量会因为叶面积指数的增加而增加,到生育期的某一时期达到最大值(与品种、栽培条件等有关),随后即使叶面积指数继续增加,产量也不会增加,即叶面积指数和产量之间呈现二次方程关系,大量的数据结果表明水稻的叶面积指数和产量之间基本呈现出正态分布的情况,另外在研究结果中显示,产量和水稻生长的各个环节的叶面积指数之间都有着一定的立体结构^[43]。然而胡法龙^[44]研究结果中,‘中龙香1号’各时期的叶面积指数与产量均呈负相关,与前人研究结果有异,其可能是水稻分蘖能力差异所造成的,由此得出分蘖能力强的水稻品种生育前期叶面积指数大不利于高产。在栽培的时候应该将重心放在控制上,而分蘖能力弱的水稻品种生育后期在叶面积指数都有利于促进产量提高,在水稻栽培的过程中选择合适的方式可以有效的提高齐穗期绿叶面积。研究也表明不同品种水稻的最适叶面积指数随生育时期的不同而不同,因此,提出了在水稻的不同生育时期保持最适叶面积指数是提高产量的有效途径。叶面积指数与产量形成的关系主要表现在:

(1)利于碳水化合物的积累;(2)利于光能利用率的提高;(3)其他条件相同时,叶面积指数达到相当数值的田块,其叶片不管是在光合强度上还是在植株的生长率上都相对较高;(4)叶面积指数的合理变化往往反映了栽培密度、水肥管理等的合理性;(5)叶面积指数相当的稻田,能合理利用地力,在一定程度上阻止杂草蔓生,降低田里水分蒸发。

8 展望

水稻的叶面积指数与产量密切相关,不局限在时间关系,还有空间关系,我们可从时间线和空间线两条主线来研究有关水稻高产的问题。水稻群体最适叶面积指数是客观存在的,在育种上提高最适叶面积指数和在栽培上使叶面积指数趋近最适值具有同等的重要性^[45]。林贤青^[46]选择使用雨水,根据实际环境在一定程度上降低水量的灌溉,对于土壤的氧化还原电位进行提升,促进地下部根系和地上部植株生长,从而使株型得到有效的改变。控制植株之间的合理间距,从而保证后期透光性,提高叶片生理功能和叶面积指数,来实现水稻的节水高产。魏永华等^[47]通过研究水分、N元素对于叶面积指数的影响,认为两者对于叶面积指数具有一定的积极影响,土壤中合理的水分会提高叶面积指数。较高的氮吸收和剑叶含氮量可以促进冠层光合强度。施氮的速度和时机对水稻产量的影响至关重要^[48]。在各氮肥条件、湿润+浅水+干湿交替三者灌溉结合的情况下,杂交水稻的叶面积率、光合速率较高,叶倾角较低,都有效的促进了杂交水稻的透光率,有效的提高了下层叶片的光合作用,更大程度的提高了水稻群体的结穗率,且抽穗期水氮互作效应最大^[49],可见合理的灌水方式和施肥条件对改善叶面积指数、增强叶片光合作用有重要作用,尤其是在抽穗期对高产起到关键作用。黄礼英^[50]研究表明在减氮条件下,相对较长的绿叶面积持续期、较优的冠层结构等能增加杂交稻花后干物质积累,使其保持高产,可见在施肥方面,氮肥减量后移,降低水稻生产成本的同时我们可以通过培育叶面积适宜的高光效群体、调整冠层结构等方法使水稻保持高产^[51]。刘军等^[52]对大穗型水稻品种高产机制和产量形成特点进行分析,结果表明大穗型水稻在齐穗期具有更高的叶面积指数。李小朋等^[53]研究表明在株行距为15 cm×30 cm和20 cm×25 cm配置下,水稻获得稳产高产,在15 cm株距时,叶面积指数变化规律与高度呈S型曲线^[54-57],在20 cm株距时,叶面积指数随着行距的增加而增大,抽穗后叶面积的衰减速度随株行距的增加而下降^[58],但处理间差异不显著,同时对于植株之间的距离进行控制,优化冠层结

构,降低倒伏危险,保障水稻高产质优。向珣朝等^[59]通过双株栽留苗的单株叶面积和叶面积指数在分蘖初期和分蘖盛期均高于其他处理。徐一兰等^[60]研究表明早、晚稻的各生育时期,抛栽叶面积指数>手插叶面积指数>机插叶面积指数,可根据实际生产情况采取不同的栽培方式来提高各生育时期的叶面积指数。播种移栽时期、水稻类型(早稻、中稻、晚稻、再生稻、多年生稻)的选择等也是突破产量的相关途径^[61-62]。

随着科学技术的发展,近年来有关叶面积指数的研究侧重于遥感、遥感数据与水稻生长模型的结合用于水稻区域产量预测、对实测产量进行回归等方面^[63-66],这对于保证粮食安全具有重要意义,同时对于精准农业的发展也具有促进作用。由于不同品种、不同生育时期叶面适宜积指数均不同,所以对高产水稻适宜叶面积指数的预测有一定难度,相信科技的发展会使我们突破局限,完成农业史上的第三次革命。

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低温对水稻光合特性的影响

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摘 要: 光合作用在农作物生长发育过程中起到至关重要的作用, 也是其产量高低的决定性因素, 而低温冷害是影响水稻生长发育和产量的严重自然灾害之一, 故前人就低温冷害对水稻光合特性影响展开了大量研究。综述了低温冷害对栽培稻和野生稻各生长发育时期包括光合速率、气孔导度、胞间 CO₂ 浓度、蒸腾速率等光合特性指标的影响。同时从选育抗低温品种、采取合理使用外源物质及改变灌水平层高度等有效栽培措施等方面提出了增强水稻抗低温能力的建议, 对保证水稻在低温冷害时维持正常产量具有指导意义。

关键词: 栽培稻; 野生稻; 低温; 光合特性; 综述

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Effects of Low Temperature on Photosynthetic Characteristics of Rice

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Abstract: Photosynthesis not only plays an important role in the growth and development of crops, but also plays a decisive role in the yield. Low temperature and chilling injury is one of the serious natural disasters that affect the growth and yield of rice. Therefore, many studies have been carried out on the effects of low temperature and chilling injury on photosynthetic characteristics of rice. In order to provide theoretical guidance for maintaining normal yield of rice under chilling injury, the effects of chilling injury on photosynthetic characteristics of cultivated rice and wild rice at different growth stages, including photosynthetic rate, stomatal conductance, intercellular CO₂ concentration and transpiration rate, were reviewed. At the same time, the prospect was put forward from the aspects of breeding low temperature resistant varieties, rational use of exogenous substances and changing the height of irrigation layer, so as to improve the low temperature resistance of cultivated rice and wild rice, and ensure that they still have normal photosynthetic capacity under low temperature conditions, which has theoretical significance for ensuring the normal yield of rice under low temperature and cold injury.

Key words: cultivated rice; wild rice; low temperature; photosynthetic characteristics; review

水稻在我国粮食作物中种植面积最大、总产量最高^[1], 是典型的喜温喜光作物, 其对温度条件敏感, 在不同的生育时期均容易受到低温冷害的影响^[2-3]。低温对水稻生产的影响不仅是农业领域研究的重点, 也一直是水稻气象研究的重点问题^[4-10]。我国水稻栽培历史悠久, 稻谷总产量居世界总产量首位, 遗传资源数量多且类型丰富, 水稻杂种优势利用研究以及杂交稻的大面积种植居世界领先地位, 对全球稻作科技的发展做出了重要贡献^[11]。在我国所有种植水稻的地区均发生过冷害, 而且重大冷害发生频率 5 a 内就有一次, 受灾严重年份水稻产量减少 50 亿~100 亿 kg^[12], 对我国粮食安全产生重大影响。光合作用是作物生长发育和产量形成的生理基础, 也是作物生产力高低的决定因素^[13]。而低温冷害对作物光合特性影响是直接导致水稻产量降低的主要原因, 当水稻遇到低温冷害

时, 光合作用削弱的同时也降低了呼吸作用, 改变膜脂过氧化与抗氧化系统, 进而降低水稻抗寒能力, 抑制水稻生长, 最终导致产量降低^[14-17]。前人就低温冷害对水稻光合特性, 包括生长发育时期光合速率、气孔导度、胞间 CO₂ 浓度、蒸腾速率等光合特性指标的影响做了大量研究。栽培稻起源于野生稻, 野生稻作为珍贵的种质资源, 具有耐冷、耐旱、抗病、抗虫、抗贫瘠、高效营养、高产优质、药用等诸多优良基因, 可以作为栽培稻改良和优良基因挖掘的重要资源^[18]。栽培稻在低温条件下光合特性也会受到影响^[19]。笔者就前人研究的低温对栽培稻和野生稻不同生育时期光合特性的影响进行综述, 为水稻耐冷品种选育和低温环境条件下水稻栽培技术措施制定提供参考。

1 低温对水稻苗期光合特性影响

1.1 栽培稻苗期光合特性研究

苗期是水稻培育壮秧的关键时期, 秧苗素质对产量的影响很大。如果水稻苗期遭遇低温冷害, 必定会影响秧苗素质, 降低产量^[20]。研究表明, 在低温胁迫条件下, 水稻幼苗的叶绿素含量、净光合速率、气孔

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导度、蒸腾速率均明显下降，叶绿素荧光参数有明显变化^[21-27]。低温胁迫下，叶片呼吸强度降低，而叶片呼吸速率（ r ）与光合速率（ p_o ）关系密切，温度越低， p_o/r 的比值越大，说明呼吸作用降低越明显^[28]，同时水稻叶片叶绿素的合成受到抑制或叶绿体功能紊乱，细胞膜透性增大，导致光合速率降低，气孔导度降低，最终导致产量下降。

1.2 野生稻苗期光合特性研究

徐孟亮等^[29]研究表明，冷胁迫后，与典型籼稻、爪哇稻，典型粳稻3种不同类型的栽培稻相比，茶陵野生稻净光合速率和光系统II光化学量子效率的变化小于典型籼稻和爪哇稻，大于典型粳稻，说明茶陵野生稻苗期耐冷性强于籼稻和爪哇稻，但弱于粳稻。黄芸香^[30]研究中与中花11（栽培稻对照）相比，干旱预处理+自然低温胁迫条件下，东乡野生稻、茶陵野生稻、柳江野生稻、海南野生稻叶绿素含量均高于对照；海南野生稻的最大光合速率、气孔导度、表观量子效率等气体交换参数以及叶绿素荧光参数均有高于对照的总趋势。陈志^[31]研究表明，茶陵野生稻苗期耐冷性与其抗氧化系统冷胁迫后的适应性变化密切相关，对低温逆境响应迅速并具有较强的恢复能力。由此可见，与栽培稻相比，大多数野生稻均有较好的耐冷性。

2 低温对水稻幼穗期光合特性影响

2.1 栽培稻幼穗期光合特性研究

水稻的幼穗期是水稻生长发育关键的时期，若在该时期遭遇低温胁迫，将直接影响水稻的产量^[32]。低温胁迫下，水稻幼穗期及其分蘖期叶片中叶绿素含量明显降低，光合速率、净光合速率、蒸腾速率明显呈下降趋势^[33-38]。

2.2 野生稻幼穗期光合特性研究

易向军^[39]研究表明，在幼穗期前的分蘖期，低温条件下，茶陵野生稻分蘖期叶片的净光合速率稍高于供试的栽培稻；其PS II最大的光化学量子效率（ F_v/F_m ）、光下PS II反应中心的激发能捕获效率（ F_v'/F_m' ）与非光化学淬灭系数（NPQ）均大于栽培稻，表现出了较强的光合作用能力；而邓志瑞等^[40]研究表明，武育粳8号生长过程中，剑叶的叶绿素含量和光合速率都高于普通野生稻，这与其他相关研究有些许不同，可能与水稻品种类型、特性及其环境等因素有关。

3 低温对水稻孕穗期光合特性影响

3.1 栽培稻孕穗期光合特性研究

水稻的孕穗期是关系到水稻产量形成的关键时期^[41]，相关研究结果表明，低温胁迫下，孕穗期栽培

稻在叶片净光合速率、气孔导度及其蒸腾速率等方面均有明显的下降趋势^[42-45]，植株最大光合速率，光饱和点及光能初始利用率随胁迫时间延长而下降、光化学淬灭系数，PS II电子传递速率及PS II最大光能转化效率呈现先降后升趋势^[46-47]。其原因可能是低温致使叶绿体的结构发生改变，表现在片层排列方向发生变化，基粒片层堆叠紧密，出现空泡甚至空洞^[48]，因而叶绿素含量和光合速率下降，造成光合同化物减少，同时暗反应受到严重损害，对栽培稻的后期生长也有很大影响，从而降低产量；相关研究表明在低温持续3 d时， L_s （气孔限制值）逐渐升高，表明此时低温导致倒2叶光合速率降低的原因主要是气孔限制因素，而在低温持续5 d时， L_s 则逐渐降低，表明此时光合速率降低的原因是非气孔因素。这与朱红^[49]抽穗后低温胁迫对水稻若干生理特性的影响研究中低温导致水稻叶片光合速率的下降的原因是非气孔因素作用的结果有些许出入。结果有待进一步研究验证。

3.2 野生稻孕穗期光合特性研究

刘凤霞等^[50]研究结果表明，东乡野生稻孕穗开花期具有较强的耐冷性；杨志奇^[51]研究结果也表明中国粳稻地方品种孕穗期耐冷性强且遗传具有多样性。由此可见，相比栽培稻而言，低温胁迫下，野生稻的光合特性会强于栽培稻，但这与野生稻及栽培稻的类型、生态环境等因素有关。

4 低温对水稻抽穗扬花期光合特性影响

4.1 栽培稻抽穗开花期光合特性研究

抽穗开花期若遭遇低温，不但影响水稻受精结实，还影响水稻叶片的光合作用和叶绿素的合成能力^[52]。研究结果表明，低温胁迫下，抽穗开花期稻株叶片叶绿素含量、净光合速率、蒸腾速率、叶片气孔导度和胞间 CO_2 浓度均有不同程度的降低^[53-55]，导致产量下降。

4.2 野生稻抽穗开花期光合特性研究

有研究指出普通野生稻耐冷性>粳稻耐冷性>籼稻耐冷性^[56]；陈大洲^[57]研究表明，东乡野生稻在抽穗开花期有较强耐冷性。低温导致水稻光合功能下降，最终导致减产，而野生稻具有较强的耐冷性，可见其光合功能下降的速率会低于栽培稻，与栽培稻相比还是具有较强优势的。

5 总 结

低温胁迫在栽培稻和野生稻的各个生长阶段都产生了影响，主要表现为对水稻叶片光合特性的影响，进而影响产量和品质。与栽培稻相比，大多野生稻具有较强的耐冷性，这与野生稻的生长环境及其适应性是密切相关的。

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(责任编辑: 张焕裕)

主要农作物品种 审定证书

审定编号：滇审稻 2018033 号

品种名称：多年生稻 23 (试验名称：PR23)

品种来源：云南大学、云南省农业技术推广总站、云南省农业科学院、景洪市农业技术推广中心、云南省种子管理站 1997 年用 RD23 与长雄野生稻杂交，经多次自交筛选，利用分子标记辅助 (MAS) 选择技术培育，2012 年形成稳定品系，定名“PR23”，2018 年定名“多年生稻 23”。

申请者：云南大学

育种者：云南大学、云南省农业技术推广总站、云南省农业科学院、景洪市农业技术推广中心、云南省种子管理站

审定意见：该品种符合云南省稻品种审定标准，同意通过审定。适宜在云南海拔 1550 米以下籼稻区种植。再生苗太多，需及早控制。

公告号：云农通告 (2018) 第 18 号

证书编号：2018-1-0033



2018 年 09 月 14 日

主要农作物品种 审定证书

审定编号：滇审稻 2020041 号

品种名称：云大 25（试验名称：PR25）

品种来源：云南大学、云南省农业技术推广总站、云南省种子管理站、景洪市农业技术推广中心 1997 年配制 RD23/长雄野生稻获得 F1 植株。2009-2016 年，利用分子标记辅助选择（MAS）技术从 F1-F14 经过多次自交筛选具有地下茎位点及丰产性、抗病性、适应性均适合的材料，于 2016 年选育出稳定品系多年生稻 PR25（Perennial Rice 25，简称 PR25）。2019 年定名为云大 25。

申请者：云南大学

育种者：云南大学、云南省农业技术推广总站、云南省种子管理站、景洪市农业技术推广中心，（胡凤益、黄光福、张石来、道金荣、李全衡、张静、吴叔康、温宪勤、黄立钰、胡建、程卯）

审定意见：该品种符合云南省稻品种审定标准，同意通过审定。适宜在云南省与区试点相似区域海拔 1500 米以下区域，注意防治病虫。

公告号：云农通告〔2020〕第 17 号

证书编号：2020-1-0041



2020 年 08 月 06 日

品种审定 品种审定

主要农作物品种

审定证书

审定编号：滇审稻 2020042 号

品种名称：云大 107（试验名称：PR107）

品种来源：云南大学、云南省农业技术推广总站、云南省种子管理站、景洪市农业技术推广中心 2014 年利用滇瑞 449 为母本，MP3-235 为父本进行杂交，获得杂交 F1 代；2015 年早稻开始，以滇瑞 449 为轮回亲本连续回交两代至 BC2F1 代；2016 年早稻开始连续自交四代，至 2017 年晚稻 BC2F4 代，材料开始稳定，材料命名为 PR54。选育过程借助地下茎相关基因进行分子标记辅助选择（Molecular Marker assisted selection, MAS）育种技术。2018 早稻定名为 PR107（Perennial Rice 107，简称 PR107），2019 年定名为云大 107。

申请者：云南大学

育种者：云南大学、云南省农业技术推广总站、云南省种子管理站、景洪市农业技术推广中心，（胡凤益、张石来、黄光福、张静、道金荣、吴叔康、李全衡、殷长生、程卯、胡建、黄立钰）

审定意见： 该品种符合云南省稻品种审定标准，同意通过审定。适宜在云南省与区试点相似区域海拔 1000 米以下区域，注意防治病虫害。

公告号：云农通告（2020）第 17 号

证书编号：2020-1-0042



2020 年 08 月 06 日

品种审定 品种审定



证书号第 2954208 号



发明专利证书

发明名称：利用长雄野生稻无性繁殖特性培育多年生稻的方法

发明人：胡凤益；张石来；黄立钰；陶大云；张静；黄光福；胡建道金荣

专利号：ZL 2017 1 0132494.2

专利申请日：2017 年 03 月 07 日

专利权人：云南大学；云南省农业科学院粮食作物研究所

地址：650091 云南省昆明市翠湖北路 2 号

授权公告日：2018 年 06 月 08 日

授权公告号：CN 106688878 B

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局长
申长雨

申长雨





证书号第 4545479 号



发明专利证书

发明名称：一种多年生稻的栽培方法

发明人：胡凤益;黄光福;道金荣;张石来;吴叔康;张静;杨旭
黄立钰;刘艳;何飞飞;刘跃明;蔡晓琳;秦世雯;高晶

专利号：ZL 2019 1 0273354.6

专利申请日：2019 年 04 月 04 日

专利权人：云南大学;云南省农业技术推广总站

地址：650091 云南省昆明市翠湖北路 2 号

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胡凤益

入选“云岭学者”





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 Qualification
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 Profession
 评审组织: 云南大学教授副教授评审委员会
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 Qualification: 副研究员
 专业名称: 物理学
 Profession: 物理学
 评审组织: 云南大学引进人才专业技
 Appraising Institution: 术职称考核认定委员会
 资格时间: 2021年07月13日
 Date of Qualification: 2021年07月13日
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 签发日期: 2021年09月14日
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Work Unit

资格名称: 副教授
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专业名称: 农学
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评审组织: 云南大学教授副教授评审委员会
Appraising Institution

认定时间: 2018年11月23日
Date of Approval

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Certificate No. _____

资格名称: **研究员**
Qualification _____
专业名称: **作物学**
Profession _____
评审组织: **云南大学引进人才专业技术职称考核认定委员会**
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身份证号: 37131119821007323X

ID Number

证书编号: 10673ZKB20006

Certificate No.

资格名称: 副研究员

Qualification

专业名称: 作物学

Profession

评审组织: 云南大学引进人才专业技
术职称考核认定委员会

Appraising Institution

资格时间: 2020年05月14日

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2金1银5铜! 创历史新高! 云大学子在第七届中国国际“互联网+”大赛中斩获佳绩

2021-10-21

2021年10月12日至15日, 第七届中国国际“互联网+”大学生创新创业大赛全国总决赛在江西南昌大学举行。经过激烈角逐, 云南大学选送参赛的8个项目分别斩获国赛金奖2项、银奖1项、铜奖5项, 金奖和奖项数量均创云南省高校和学校历史最好成绩, 学校还首次荣获“高校先进集体奖”, 成绩斐然。



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新闻聚焦

科技小院“智慧稻”助力乡村振兴

来源: 云南日报 2021-04-24 09:45:54 【字体: 大 中 小】

目前,全球一半以上的人口以稻米为主粮,奠定了稻谷是世界上最重要的粮食作物的地位。稻谷生产的环境友好型栽培技术的创新研究,是全球农业和绿色发展备受关注的重要领域。

1997年,云南大学胡凤益团队提出了利用长雄野生稻地下茎无性繁殖特性培育多年生稻的设想。经过20多年的探索和实践,培育出了具有生产应用价值的多年生稻23、云大25等多个多年生稻品种,从物候、土壤生态等多方面开展了试验、示范和推广试验,取得重大突破,在全球多年生作物育种领域具有里程碑意义,实现了稻谷生产方式从一年生到多年生的转变。

高校肩负人才培养、科技创新、社会服务、文化传承等使命。让多年生稻技术快速走进农户,走进乡村,田野吐出稻花香,农民增产又增收,成为了胡凤益团队的衷心期待和不懈实践。

2020年,胡凤益带领多年生稻研发团队在西双版纳傣族自治州勐海县勐遮镇曼恩村委会的曼拉村建立了多年生稻科技小院。小院试验田50余亩,多名研究生和老师长期入驻。研发团队以小院为载体,把农业科技研发和农科人才培养相结合,为乡村振兴培养主力军。

“这种杂草叫做狗牙根,是一种稻田恶性杂草,防治它们一定要趁早,要在水稻4叶期、杂草2-3叶期施药……”小院的同学们将自己所学的生产知识传授给农民,同时也向农民们学习经验,不断完善自己的专业技能。同学们把科学技术带到了田间地头,将书本知识和生产实践相结合,为多年生稻技术发展提供了保障,同时也为新型农科人才培养注入了新生力量。

小院的同学们和老师们积极服务于当地的农民和新型经营主体,通过新型经营主体为农民带来了实际收益。小院与西双版纳宝云香稻公司展开合作,公司应用多年生稻5万多亩,为企业节约了种子和劳动力等生产成本开支,带来了直接经济效益1160万元。以多年生稻技术为核心,以多年生稻科技小院为载体,在我省14个州市的76个县区、全国南方8个省以及“一带一路”倡议沿线的老挝、缅甸、柬埔寨、孟加拉国、巴基斯坦、乌干达、科特迪瓦、塞拉利昂等国家开始试验示范,累计推广多年生稻10万多亩,惠及2.3万农户。

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实践勤耕读 成长“慧”种稻----记云南大学多年生稻科技小院人才培养

2021-04-24

一棵稻，从昨天走来

全球一半以上的人口以稻米为主粮，奠定了稻谷是世界上最重要粮食作物的地位。而稻谷生产中环境友好型栽培技术的创新研究，则是全球农业和绿色发展备受关注的重点领域。



云南典型的水稻种植模式

1997年，云南大学胡凤益团队提出了利用长雄野生稻（*Oryza longistaminata*）地下茎（Rhizome）无性繁殖特性培育多年生稻（Perennial Rice, PR）的设想。经过二十余载的不断探索实践，培育出了具有生产应用价值的多年生稻23（PR23）、云大25（PR25）、云大107（PR107）等多个多年生稻品种。从物候、土壤生态等多方面开展的试验、示范和推广试验，取得重大突破，在全球多年生作物育种领域具有里程碑意义，实现了稻谷生产方式从一年生到多年生的转变。多年生稻技术是一项轻简化的稻作生产技术，多年生稻的秧苗是从上一年（季）稻植地下茎的芽上生长出来。实现了从第二年（季）起，基于越冬和免耕技术，稻谷生产不再需要买种、育秧、犁田耙田、栽秧等生产环节，促进了节本增效、减少劳动力投入、减轻农田水土流失等多维效益协调发展。

高等教育肩负着人才培养、科技创新、社会服务、文化传承的使命。让多年生稻技术快速走近农户，走进乡村，让田野吐出稻花香，农民增收又增收，是云南大学胡凤益教授团队师生不懈努力的目标。

建小院，扎根在乡村

新农科如何培养人才？在全国农业专业学位研究生教育指导委员会立项重点课题的支持下，云南大学农学院胡凤益教授带领多年生稻研发团队，自2020年始立足服务国家脱贫攻坚和乡村振兴战略，秉承农业可持续绿色发展理念，遵循就地合作科技服务生产宗旨，推动农科学子“学农爱农”实践育人模式创新，在云南省西双版纳州勐海县勐遮镇曼恩村委会的曼拉村建立了多年生稻科技小院。小院有试验田50余亩，常年有5-7名研究生和2-3名老师入驻。以小院为载体，将农业科技研发与农科人才培养进行结合，培养农科学子的三农情怀、促进学生德智体劳全面发展，努力实现让农科学子成为祖国乡村振兴建设的主力军。



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- 云南省第一个应用数学中心获批成立 12/27
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- 化学科学与工程学院在重(贵)金... 12/16
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- 云南省地球系统科学重点实验室... 12/13
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云南多年生稻实现“一种多收”

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【打印】

全国农业教指委重点课题“云南高原特色农业科技小院开放共享运行实践与机制研究”交流会暨科技小院授牌仪式顺利举行

发布日期：2021-04-30 浏览次数：37864

4月23-25日，全国农业教指委在云南省西双版纳勐海县和昆明市阳宗南国山花有限公司的两个科技小院所在地，举行教指委重点课题“云南高原特色农业科技小院开放共享运行实践与机制研究”交流会暨科技小院授牌仪式。全国农业教指委委员兼秘书长李健强教授，云南大学赵琦华副校长、研究生院常务副院长王启梁、“双一流”办公室陈善江处长，云南农业大学赵乐静副校长，中国农业大学教授、中国农技协科技小院联盟秘书长李晓林教授，教指委重点课题负责人云南农业大学谢世清教授、子课题负责人云南大学农学院院长胡凤益教授及其团队成员等5个子课题承担单位近70人参加了会议交流和挂牌仪式。

在西双版纳景洪县和勐海县，课题专家组参观考察了云南大学建设的多年生稻科技小院。在全国农业专业学位研究生教育指导委员会立项重点课题的支持下，胡凤益教授带领多年生稻研发团队，立足服务国家脱贫攻坚和乡村振兴战略，坚守生产一线10余年，在西双版纳州勐海县曼拉村建成了多年生稻科技小院。小院依托云南大学试验站，建有试验田50余亩，常年有多名研究生和教师入驻。农业硕士在就读期间以多年生稻的种质选育、栽培和施肥、病虫害和杂草防控、增产增收等实际问题为科研课题，以解决产业需求问题为工作目标，推动产学研融合、科技服务生产。团队与西双版纳宝云香稻公司合作，积极服务于当地的农民和新型经营主体，给农民带来了实际收益。李健强和王启梁等一行与驻院研究生交流，考察了小院研究生的科研和生活条件；为重点课题建在勐海的多年生稻科技小院授牌。

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中国科学院种康院士、中国水稻研究所钱前研究员等专家考察指导云南大学多年生稻研究工作

2019-05-05



2019年4月24日,中国科学院种康院士、中国水稻所副所长钱前研究员、国家杂交水稻工程技术研究中心袁隆平助手辛业芸研究员、中国科学院遗传发育所王静处长一行到云南大学西双版纳多年生稻试验基地考察指导工作。云南大学农学院院长胡凤益研究员、景洪市农业技术推广中心程卯主任、勐海县农业技术推广中心朱二主任、勐遮镇农业技术推广中心王春荣副主任、西双版纳宝云香稻农业发展有限公司许宝柱总经理及相关工作人员参加此次现场考察活动。

专家组一行考察了位于勐海县勐遮镇多年生稻试验示范点,包括曼根村委会曼板竜试验点、曼根村委会曼刚村小组试验点、曼根村委会曼根村、曼恩村委会曼拉试验基地。在景洪市嘎洒镇多年生稻育种基地,胡凤益研究员从多年生稻遗传机理研究、多年生稻品种选育、多年生稻栽培生理、多年生稻栽培技术、多年生稻生产应用、多年生稻目前存在的问题等进行了汇报。种康研究员作了题为“作物感知低温信号机制与分子设计潜力”报告。种康院士在报告中指出,多年生稻技术作为一种新的稻作生产模式,是稻作生产技术中原创性、颠覆性的研究工作,目前已经取得较大进展,同时还应加大遗传规律、耐冷特性等相关研究,进一步加快多年生稻生产应用步伐,为粮食安全发挥应有的作用。

农学院 供稿

(编辑:李哲)

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云南大学多年生稻服务地方农业发展，助力脱贫攻坚战

来源：云南大学农学院 发文时间：2018-01-23

云南省玉溪市元江哈尼族彝族自治县澧江镇南洒村委会行政村，地处澧江镇东南面，是元江县贫困村之一，居住人口主要以哈尼族、彝族、傣族为主，以种养殖业作为主要经济来源，制约该村发展主要因素包括农业产业结构单一、种养殖技术落后等。多年生稻作为一种绿色轻简化栽培模式，具有省工、省时、节约成本等优点，种植多年生稻能解决贫困户口粮问题，同时能最大限度将农户从繁重的田间劳动中解脱出来从事其他产业，为打赢脱贫攻坚战保驾护航。云南大学农学院、云南省农业技术推广总站、云南省玉溪市元江哈尼族彝族自治县农业局合作达成协议，服务该区域农业发展，在该区域种植200亩左右多年生稻，提供免费提供农户多年生稻种子、化肥补贴、技术培训、跟踪技术指导等方式助力该村脱贫攻坚。

2018年1月8日，云南大学农学院黄光福、云南省农业技术总站吴叔康总农艺师、元江县农业技术推广站站长陈亮新等，前往元江县农技站组织澧江街道那塘村民在那塘村召开多年生稻栽培技术培训会，参会农户有70多人，云南大学农学院黄光福老师，云南农技推广总站吴叔康总农艺师对多年生稻的栽培规格、肥水管理、病虫害防治等技术进行详细讲解。参会人员现场提问，培训人员现场解答，农业对多年生稻概念，多年生稻栽培技术有了深刻认识，为多年生稻种植打下坚实基础。同时现场完成种子发放工作，多年生稻正式开启在该区域服务农业发展的步伐，助力该村脱贫攻坚战。



图1 培训人员合影



图2 培训会现场



图3 多年生稻种子发放

成果媒体宣传

像种韭菜一样种水稻！云南多年生稻实现“一种多收”

人民日报客户端云南频道 叶传增 2021-10-24 19:50 阅读量44.8万

割完一季接着长，一次栽种能连续收割多年。在云南，有这样一种多年生稻品种，可以让农民像种韭菜一样种植水稻。

金秋时节，云南省元江县澧江街道南洒村梯田种植的300亩多年生稻“云大107”一片金黄。24日，经农业农村部水稻专家组田间测产验收，该品种晚稻亩产464.8千克，加上7月份第一季早稻测产的亩产655.65千克，今年该品种多年生稻亩产达到1120.45千克。这是迄今为止多年生稻“云大107”在云南大面积推广种植的最高产量。



农业农村部水稻专家组宣布测产验收结果 王崑摄影

据了解，“云大107”多年生稻由云南大学胡凤益教授团队培育。在云南省科技计划等项目支持下，该团队历经20多年艰苦探索，发明了利用长雄野生稻无性繁殖特性培育多年生稻的方法，原创性构建了多年生稻育种理论体系和耕作栽培技术体系，实现了多年生粮食作物育种从“0到1”的突破，是水稻育种和栽培技术的补充和完善，为水稻的绿色生态低碳发展开辟了一条新途径。

胡凤益介绍，多年生稻在适宜区域只需种植一次，从第二年（季）起无需再购种、育秧、犁田、耙田、插秧，只需要做好田间管理就可实现连续多年（季）的水稻轻简化生产。

“每亩节约5-6个人工，按每个人工100元计算，从第二年（季）起每亩可节约500-600元的人工成本，显著地减少了种子和劳动力投入、精简了许多繁琐的生产环节，降低了稻农的劳动强度，且产量保持相对稳定，突破了传统水稻的耕作方式，实现了水稻的轻简化生产。”胡凤益说。



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云南大学致力研发可反复收割的多年生水稻

2016-06-06 来源: 浙江在线 编辑: 谢江平 作者:

浙江在线·教育新闻网 5月31日讯(记者成亮) 5月31日下午,“2016全国重点网络媒体云南高校行”媒体团走进云南大学,该校大力研发的多年生水稻技术令记者们印象深刻。

多年生水稻听起来有点神奇。这是怎样的水稻?据了解,多年生水稻可以像种果树一样,一次播种多年收割。近年来,云南大学农学院胡凤益研究员带领团队选育出多年生水稻,目前正在开展遗传改良、技术跟进、市场推广等方面的工作。

“种一次水稻可以多年收割。”这听起来像是梦想,但其在云南已经成为现实。长雄野生稻起源于西非,拥有发达的地下茎,有较强的病虫害抗性,为多年生草本植物。云南大学农学院研究员胡凤益联合云南省农科院粮作所等单位,利用幼胚挽救的方式成功配置,并获得了RD23/长雄野生稻杂交种F1代。选育很多后代群体。同时,利用长雄野生稻地下茎的多年生性状,培育了一系列多年生品种。多年生水稻可以越冬,而大多数再生稻不能越冬。

在西双版纳等双季稻地方,这种多年生水稻一年可收割两次,而在单季稻地方,一年只能收割一次,种了多年生水稻后,只要不破坏地下茎,免耕,还可套种蔬菜、小麦等作物。多年生水稻的稻米属于粳稻米,产量和一般的常规稻相当,每一季每亩可产500-600公斤,从第二个季节开始,生产环节和投入减少一半以上,表现在不需要购买种子、不需要育秧、不需要栽秧、不需要犁田耙田,不但简化生产,而且减少劳动力的投入,适应机械化操作,经济效益好。南亚东南亚大部分属热带稻区,一年两季,可以连作。

胡凤益研究员培育的多年生水稻已商业化推广5000亩,在云南普洱、孟连、景洪、勐海等地试验种植,有些品种多年生性强,一次播种可收割四五年,具有很好越冬能力,产量表现稳定。去年早稻亩产449.5千克,晚稻亩产450.2千克。

基于多年生水稻项目在科技创新服务云南经济社会发展方面的巨大潜力,云南大学已获批建设云南省多年生水稻工程技术研究中心,通过高端科研平台进一步开展研发工作。前不久,胡凤益研究员还前往老挝,在万象实验基地、琅勃拉邦试验基地现场考察多年生水稻的试种情况。多年生水稻正在走出国门。未来,多年生水稻将造福更多的人。

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像种韭菜一样种水稻！多年生稻“云大107”创云南“一种两收”最高产量

发布时间：2021年10月24日 18:40:00 来源：云南网



多年生稻“云大107”

云南网讯（记者 陈云芬）金秋时节，云南省元江县漕江街道南洒村梯田种植的300亩多年生稻“云大107”一片金黄。10月24日，农业农村部水稻专家组对云南大学、云南省农业技术推广总站、玉溪市农业科学院及元江县产业发展中心等单位组织实施的多年生稻“云大107”示范区进行了田间测产。测产结果显示：百亩连片晚稻平均亩产464.8千克，加上7月份第一季早稻测产的平均亩产655.65千克，一年“一种两收”稻谷平均亩产1120.45千克。这是迄今为止多年生稻“云大107”在云南大面积推广种植的最高产量。



像种韭菜一样种水稻

“像种韭菜一样种水稻，割了又长，种一次可以连续收割三五年，亩产量超过1000公斤，这就是多年生稻。”云南大学胡凤益教授介绍，多年生稻在适宜区域只需种植一次，从第二年（季）起无须再犁耙田地、买种子、播种、育秧和栽秧，只需要做好田间管理就可实现连续多年（季）的水稻轻量化生产。每亩可节约5至6个人工投入，按每个人工100元计算，从第二年（季）起每亩可节约500元至600元的人工成本，显著地减少了种子和劳动力投入，精简了许多烦琐的生产环节，极大地降低了田间劳动强度。南洒村主要农业产业以水稻生产和养牛为主，种植多年生稻可以实现种一年收2季稻谷和3次稻草，还可连续种植多年。多年生稻“一种两收”模式既解决了南洒村人的口粮问题，又解决了牛的饲草问题，达到了稳粮增收的目标，成为乡村振兴产业可持续发展的典型模式。



多年生稻“云大107”创云南“一种两收”最高产量

据介绍，云南大学胡凤益团队联合相关单位，在云南省科技计划等项目支持下，经过20多年的艰苦探索，发明了利用长雄野生稻无性繁殖特性培育多年生稻的方法，原创性构建了多年生稻育种理论体系和耕作栽培技术体系，实现了多年生粮食作物育种从“0到1”的突破，为水稻的绿色生态低碳发展开辟了一条新途径。

截至目前，云南大学已经培育出了“多年生稻23”“云大25”“云大107”等适应多个生态区的多年生稻品种。其中，“多年生稻23”于2018年通过云南省审定，是全球第一个通过审定的商业化生产应用的多年生作物品种，在多年生作物育种中具有里程碑意义。全国农业技术推广服务中心自2018年组织在全国南方稻区的河南、湖北、江西、湖南、广东、广西、贵州、云南、海南等省（自治区）对多年生稻进行试验示范，已累计试验示范应用12万多亩。多年生稻技术也已在“一带一路”倡议沿线的老挝、缅甸、泰国、孟加拉国、伊朗、乌干达、埃塞俄比亚等国家开展试验示范，显示出巨大的发展潜力和广泛的应用前景，为世界稻作生产贡献了中国智慧和方案。

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玉林率先在全区大面积示范种植多年生水稻

日期: 2019-03-27 10:26 作者: 黎颖 杨光登 来源: 北流市农业局

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20日上午, 玉林市农业技术推广站组织农技人员, 在北流市大里镇古红村开展多年生水稻大田播种工作, 创建“玉林市多年生水稻示范片”。

玉林市农技站高级农艺师罗学夫介绍, 该示范片面积约50亩, 水稻生长期为3年, 是玉林市也是广西全区创建的第一个大面积栽培多年生水稻示范片。罗学夫说: “多年生水稻一次播种, 可以收获6次, 即收三年。大面积的示范(种植多年生水稻)主要是观测在大面积的情况下多年生水稻将会遇到什么样的技术问题。”

专家介绍, 多年生水稻即一次性种植后, 可连续生长两年或两年以上的水稻。玉林市农技推广站从云南引进多年生水稻种子, 并经成功试验种植表明: 多年生水稻在稻谷年产量、稻米品质、田间管理、病虫害防治等各方面与传统水稻没有多大差别。如果大面积示范栽培多年生水稻成功, 就可以进行大量推广种植, 这对于提高水稻生产效率非常有意义。

据了解, 多年生水稻, 一次播种以后, 能够收割三年6造。种植多年生水稻可以节约种子成本和耕种成本。

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多年生稻是何物？来一起涨知识！^{媒体宣传}

央视新闻客户端 | 2021-10-24 23:25:44 浏览量31946

多年生稻是种一次可以连续收割二次、三次，甚至两年、三年，实现多年生长的水稻，是利用非洲长雄野生稻与云南本地品种杂交选育出来的，是一种创新，现在的水稻基本一年生，种一次收一次，而多年生稻可以种一次收多年，这不仅减轻了老百姓的田间劳动强度和劳动投入，更是一种轻简化的稻作生产技术。



10月24日，全国多年生稻现场观摩及测产验收会在云南玉溪元江县召开，来自全国各地的农业技术专家和技术人员齐聚一堂，对当地300多亩的多年生水稻，进行研究测产验收。此次验收的300多亩多年生稻，是由云南大学胡凤益教授团队培育的多年生稻“云大107”，该项目2021年开始在元江县开始大规模推广应用，为以哈尼梯田为主的千年稻作生产方式提供了更多可选方案，为种植区域的乡村振兴贡献了新的农业科技模式。



胡凤益教授团队是从1997年开始探索研究多年生稻，经过24年的探索研究，把野生种水稻的某些现状恢复到家种水稻里，育成了多年生水稻品种，是全国水稻育种的一个创新；2016年开始田间试验，经过几年的试验种植，在水稻的适应性、稳定性和丰产性及病虫害防控等各环节均获得了成功。多年生稻的成功离不开科研团队的坚持和奉献。

经专家组的实试验收，元江县300亩“云大107”多年生稻的晚稻验收结果是亩产464.8千克，根据玉溪市农技推广中心早稻的测算结果是（亩产）655.65公斤这样两季的平均产量就是（亩产）1120.45公斤，收获颇丰超出预期目标。

云南频道 > 云南快讯

玉溪市推广种植“多年生稻”实现丰产丰收

2018-07-17 10:07:00 来源:

央广网玉溪7月17日消息（玉溪台 白兴学）今年，玉溪市元江县引种试种300亩“多年生稻”长势喜人，眼下已进入收割期。经测产，最高亩产达719.97公斤，平均亩产667.08公斤，比邻近非示范区种植的杂交籼稻品种增产7.38%。

据了解，“多年生稻”俗称“韭菜稻”，这种稻子栽在田里，能像韭菜一样割了又长，长了又割，只需栽种一次就可连续收割几年或更长时间，产量还能保持相对稳定。目前，云南省有14个州市22个示范点种植1万亩左右的“多年生稻”。

编辑：张江元



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2019年南亚东南亚多年生稻技术交流研讨会顺利召开

来源：云南大学农学院 发文时间：2019-07-01

2019年6月24日至6月30日，云南大学农学院多年生稻研发团队组织召开了多年生稻技术面向南亚东南亚国家应用的国际研讨会，会议邀请了柬埔寨、老挝、缅甸、孟加拉、泰国、越南等南亚东南亚国家及澳大利亚的农业研究院（所）代表共计21人前来参加。

参会代表6月25日至6月27日到西双版纳进行多年生稻现场观摩交流。我方多年生稻研发团队就多年生稻种植情况进行了详细讲解，各国代表均表示多年生稻技术是一项绿色的轻简化稻作生产技术，它的推广及应用为保障南亚东南亚粮食安全具有重要意义。

6月29日，在云南大学农学院进行会议研讨，各国代表依次进行了发言，深入交流了多年生稻试验示范方面的经验和成果，并对试验示范中遇到的困难和问题进行集中研讨。最后，我院多年生稻团队就多年生稻技术在南亚东南亚推广及应用进行了战略部署，各国代表均达成一致意见。

本次会议的顺利召开，进一步促进了我方与南亚东南亚各国之间的交流与合作关系，推动了多年生稻在南亚东南亚的推广应用。

供稿人：付琦，杨智梅



图1 西双版纳景洪多年生稻试验基地参观学习



图2 西双版纳景洪多年生稻试验基地参观学习



图3 西双版纳景洪多年生稻试验基地现场观摩培训



图4 云南大学国际合作与交流中心副处长中成欢接待群



图5 合影

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勐腊县组织参加“2019年多年生稻新品种新技术现场观摩”培训会

2019-07-12 00:00

(来源: 西双版纳州勐腊县人民政府)



6月27日, 勐腊县农业技术推广中心技术员参加了在勐海县召开的2019年多年生稻新品种新技术现场观摩培训会。该多年生稻项目由云南大学和云南省农业技术推广总站牵头组织实施。2019年勐腊县栽培多年生稻面积合计120亩(其中: 易武镇100亩, 勐捧镇20亩)。观摩培训之后, 勐腊县农业技术推广中心组织勐腊县种植多年生稻的农户到勐海县进行现场观摩学习。现场观摩勐海县勐遮镇水稻生产示范、云南大学曼拉田间试验站等的水稻品种及技术试验现场。通过现场观摩学习, 提升了农户种植水稻的热情, 掌握了水稻种植的新技术、新方法。

撰稿: 杨海燕、丁海华 校对: 杨文 刘春艳 审核: 王燕 [返回搜狐, 查看更多](#)

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孔板波纹规整填料



每日一笑: 妹子衣服穿的这么少, 就不怕晒黑了吗

大家都在搜: 专家称取消公摊或影响购房



股市经典口诀: “换手率”涨三不追, 跌四不压. 看广告

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每日一笑: 妹子衣服穿的这么少, 就不怕晒...



戴笠49岁自杀前坦言: 我一生只佩服2个...



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快看！防城港有一种“韭菜”般神奇的多年生水稻，一次播种连续收割多年！

2019-07-22 15:25

“如果说得简单点，我们的这项研究可以让农民‘懒’一点，但收入可以更多一点。”7月15日，当到我市参加新农业新技术讲座的云南大学农学院院长、教授胡凤益说出这句话的时候，一旁的好几个人还一脸疑惑。



7月16日，胡凤益在我市举办的新农业新技术讲座上着重阐述了“多年生稻技术研发与应用”。

胡凤益进而解释：“20多年来，我们团队一直在做多年生稻的研究，它就像韭菜一样，可以割了又长，长了又割，农民只需栽种一次就可连续收割几年或更长时间，期间不需要再购买种子、育秧、犁田、耙田、插秧，极大地减少了劳动力的投入，降低农民的劳动强度，产量还能保持相对稳定，突破了传统稻作方式，是实现稻作轻量化生产、推动种植业结构转型升级的新途径。这个过程节省出来的时间，农民可以用来发展更多的产业，增加收入。”

“原来如此。”一旁的几个人恍然大悟。

多年生稻，顾名思义，即通过人工培育，在生产条件下能反复利用地下茎正常萌发再生成苗实现多年种植的稻。

从1997年开始，当时还在云南省农业科学院粮食作物研究所工作的胡凤益就带领团队开展了多年生稻的研究。如今，多年生稻的科研成果已走在世界前列。

如何把一年生栽培稻变成多年生稻呢？秘密就藏在长雄野生稻的基因中。长雄野生稻是起源于非洲的一种野生稻。胡凤益团队把栽培稻和长雄野生稻杂交，对后代进行以地下茎为主的多年生性状选择，培育出具有多年生性的中间品系，成为多年生性供体。之后，再把这些供体与主栽品种杂交，利用分子标记辅助选择育种技术，在后代中快速选择有长雄野生稻地下茎基因位点的品（系）种。

通过多年的研究，胡凤益团队终于解开了长雄野生稻多年生性的遗传秘密，获得了携带来自长雄野生稻多年生性基因中间育种材料。目前，他的团队已选育了多个多年生稻品种（系）。

从2015年开始，胡凤益团队选育出来的部分多年生稻品种（系）开始在云南省多个稻区进行试验种植。2017年，又在我国南方8个省（市）的10个县（区）进行适应性试验种植。其中，我市就属于适应性试验种植示范区之一。

“2017年，我们在防城区和东兴市试种的0.6亩多年生稻都被鸟儿吃了，敲着锣都吓不跑它们，真是可惜啊。不过，今年在上思县试种的200多亩多年生稻长势喜人，即将进入收割期。”市农业技术研究员刘义明面露喜悦地说：“目前，在我市试种的一共有3个多年生稻品种（系），可以说已经是试种成功，下一步将逐步扩大种植面积。”

7月16日，第八届百名博士防城港行农业农村局分团成员在讲座之余向胡凤益请教多年生稻的知识。

大家都在搜：新娘穿自己设计全粉婚纱



股市经典口诀：“换手率”涨三不追，跌四不压。看广告

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我军击毙越军狙击手，一看死者面容，个个... 每日一笑：妹子衣服穿的这么少，就不怕晒...



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上思多年生稻试种成功

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广西日报

2019-08-16 12:13 | 广西日报官方帐号

关注

本报上思讯 近日，在上思县那琴乡那琴村、那琶村、上思县农科所试验基地试种的多年生稻早造喜获丰收。农技人员经现场取样测产表明，该稻谷在上思试种成功。

多年生稻由云南大学农学院院长、教授胡凤益带领团队研发，已在云南省推广种植。多年生稻可以实现连季生产，农民只需栽种一次就可连续收割几年或更长时间，期间不需要再购买种子、育秧、犁田、耙田、插秧，减少劳力、资金、时间的投入，极大地解放生产力，是实现稻作轻简化生产、推动种植业结构转型升级的新途径，让“农民‘懒’一点，收入多一点”成为现实。

去年，防城港市开始引进多年生稻进行小面积试种。今年，该市共引进了PR23、PR25、PR107三个多年生稻品种，在上思县用200多亩田地试种。在此次早造收割中，农技人员从上述3个点取样测产，3个品种的产量分别为425公斤、425公斤、350公斤干谷，亩产在广西各试种区中最高。

“我们引进多年生稻，可以有效地把农村闲置的农田利用起来，增加粮食产量，让粮食安全多一份保障。”防城港市农业技术研究员刘义明说，“现在产量有了，下一步就是谋划如何打响特色品牌，拓宽销售渠道，提高产值，从而增加农民收入。”

(朱新华 韦佐)





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灌阳试种多年生稻初获成功

2019-09-06 16:32

(来源：桂林市灌阳县人民政府)

多年生稻是我国近年来研究出来的一个新型稻种，灌阳县经过3年的试验示范已初步获得成功。

9月4日，笔者在灌阳县新街镇戈洞村看到，自治区推广站副站长李明灌等专家深入田间，认真察看多年生稻一季收获后再生苗的生长情况，并俯下身子仔细观察了2018年种植的PR25多年生稻稻桩的情况。笔者在现场看到，多年生稻在外观上与其他水稻并没太大区别。

发展多年生稻可减少水土流失，是稳定粮食生产、确保口粮安全的需要，是实现稻作轻简化生产、丰富耕作制度的需要，是实现水稻生产节本增效、推进绿色发展的需要。多年生稻可以实现连季生产，像韭菜一样割一茬长一茬，种一次可以连续收获三至四年，期间不需要再购买种子、育秧、犁田、耙田、插秧，减少劳力、资金、时间的投入。据农业专家介绍，如何让桂北灌阳种植的多年生稻稻桩安全越冬是一个主要问题。此外，多年生稻一季如何清除田间杂草也需进一步探索加以解决。

据了解，该县2017年开始引进多年生稻试种，当年稻桩被冻死。2018年引进多年生稻PR25小面积试验，一季亩产超1000斤。2019年示范种植PR25面积5亩多，一季亩产一般在900斤左右。

9月4日，区推广站副站长李明灌（左二）等领导专家察看2019年传统育秧与手插的多年生稻

2018年种植的多年生稻PR25抽穗期

2018年种植的多年生稻一季收获后的稻桩

2019年种植的多年生稻PR25与其他稻的品比试验

领导、专家们现场察看2018年种植的多年生稻一季收获后的稻桩 [返回搜狐](#)，[查看更多](#)

原文链接：[灌阳试种多年生稻初获成功](#)

声明：该文观点仅代表作者本人，搜狐号系信息发布平台，搜狐仅提供信息存储空间服务。

桂黔两省农技推广部门现场观摩考察指导云南多年生稻技术试验示范及推广应用工作

来源：云南大学农学院 发布时间：2019-12-21

在全国农业技术推广服务中心的指导下，从2017年，在南方熟区开展了多年生稻技术的试验示范工作，取得了重要进展。为进一步加快多年生稻技术在贵州黔（桂）试验示范及推广应用，2019年12月16-19日，贵州农业技术推广总站马泽新站长和广西区农业技术推广总站农土发站长组织并带队各省级相关州市农业技术部门及农业企业一行24人，现场观摩考察指导云南元江县、越海县、普洱市多年生稻技术试验示范核心区及云南大学多年生稻技术田间试验示范研究基地、贵州农业厅种植业处新调研员、贵州种子管理站马世义调研员、广西站李明副站长、贵州总站李明副站长、云南省农业技术推广总站、玉溪市农技中心张忠主任、西双版纳农技中心高八副主任、元江县农技中心陈高副主任、云南大学胡凤益院长等全程陪同考察。

此次现场观摩考察指导交流活动，加深了对多年生稻技术的认识和共识，促进和完善了云南大学多年生稻技术研发工作，促进了多年生稻技术在贵州黔（桂）试验示范及推广应用。

（供稿：黄兴福）2019年12月20日



图1 考察组在越海县稻电试验示范指导工作



图2 考察组在越海县拉云南大学多年生稻研究基地考察指导



图3 贵州考察组考察指导越海多年生稻 23 (PR23) 示范



图4 考察组考察指导景洪酒海多年生稻技术研发基地



图5 考察组考察元江县多年生稻技术示范现场



图6 广西考察组考察元江县多年生稻技术 PR107 示范现场

多年生稻在云南镇沅“开枝散叶”

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云南网 2020-05-28 12:52 | 云南网官方帐号

关注

云南网讯（通讯员 汤国景）多年生稻是近20年来云南大学通过分子育种技术选育出来的，具有宿根性特点及多年生性的水稻种，具体表现为栽培一年可在3年至4年中持续收稻。

云南普洱市镇沅彝族自治县拉祜族自治县在海拔1200米以下的河谷坝区就种植着多年生稻，目前可有一年两熟、亩产吨粮的收获。



“免耕”栽培技术。汤国景 摄

据了解，多年生稻免耕种植技术具有节省购种、育秧、犁耙田、移栽等优点，成本降低、利润增加对种粮农民来说意义重大，同时免耕技术对保护农田生态环境，促进农业可持续发展具有深远的意义。

镇沅县农业技术推广中心自2017年以来，与云南大学农学院合作，引进多年生水稻8个品种，进行不同区域品比试验和品系试验，经过4年的跟踪观察，筛选出了PR23、PR107两个适宜镇沅推广种植品种，该品种性状稳定、抗性好、越冬能力强、产量高、品质中上。2018、2019连续2年在勐大桂花甲、半坡、平地、大井实施种植210亩，第一年（单季）平均亩产500公斤以上。



“免耕”栽培技术。汤国景 摄

2020年，镇沅在勐大镇文卜、大井村新植50亩多年生稻示范样板，目前，长势良好，通过示范样板带动下，有望逐年增加播种面积。

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2.77万次播放 | 2020年6月3日

66

297

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云南多年生水稻像韭菜，种一次可连续收割三四年



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陷女孩偷了5万块钱

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多年生稻试验项目落户彦洞乡

字体: 小 **中** 大 发布时间: 2020-06-21 11:00:40 文章来源: 彦洞乡 作者: 罗唯眼 打印本页 关闭本页 访问量: 12次

为解决当地青壮年劳动力外出务工后农村劳动力缺乏问题, 锦屏县农业农村局从外地引进多年生稻项目进行生产试验。试验地选择在彦洞乡教民村, 试验面积0.1亩, 试验品种2个, 目前秧苗长势良好, 各项试验观察正在有序进行中。



多年生稻属再生稻品种, 移栽1年后即可连续收获多年, 能够有效地解决彦洞地区青壮年劳动力外出务工后农村务农人员减少, 水稻种植生产成本增多, 稻田抛荒严重的问题。当地群众对多年生稻种植非常欢迎。



上一篇: 平略镇三个示范点争创环境卫生村寨
下一篇: 固本乡: 同心相扶手, 共谋产业兴

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全省多年生水稻技术培训会在我县召开

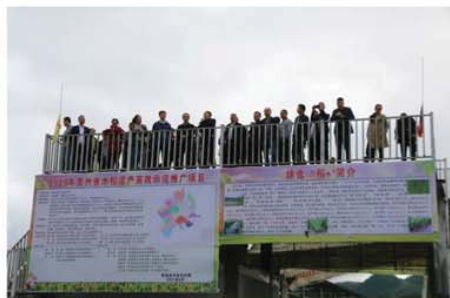
时间: 2021-04-28 14:37:47 来源: 思南县人民政府 点击量: 12次

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4月26日,全省多年生水稻技术培训会在我县召开。会议为不断总结完善多年生稻耕作栽培技术,丰富稻田耕作制度,扩大其在适宜地区的推广应用,努力推进水稻生产的绿色发展起到了积极的促进作用。



会前,参会人员观摩了塘头镇“绿色稻+”试验、示范基地,参观了多年生稻示范展示现场,项目研究团队人员介绍了项目研究进展情况、最新成果,实地了解了多年生稻在我县的试验示范情况,并围绕相关问题进行了现场交流。



培训会上,全国农技服务中心首席专家程映国研究员、云南大学农学院胡凤益研究员就多年生稻原理作了系统讲解和技术培训,省农推站介绍了贵州多年生稻技术研究情况,思南、从江、余庆分别作了经验交流。



多年生稻实现一种两年四收

广西日报 2020-12-03 10:11 | 广西日报官方帐号 关注

近日，自治区农业农村厅组织中国水稻研究所、贵州省农技推广总站、自治区农科院水稻所等单位专家到上思县，对多年生稻示范及推广应用项目进行田间测产验收。

专家组一行来到上思县思阳镇昌墩村试验示范点，通过听取项目情况汇报、现场测量面积、实测测产等方式，对试验示范种植的多年生稻进行现场测产验收。

云南大学农学院院长、研究员胡凤益介绍，多年生稻种一次可以收2-3年，从第2年开始，老百姓不用买种子，不用犁田，不用撒秧、育秧、插秧，能够节约劳动力成本。

据了解，上思县农业科学研究所多年生稻试验示范点是云南大学农学院、自治区农业技术推广站联合实施“多年生稻种质创新及应用研究”项目点，面积17.65亩，种植云大25、云大107、PR23三个品种，其中云大107、PR23是第一年第二茬，云大25是第二年第四茬。

“引进这几个品种，技术经过一系列探索研究，逐步走向成熟。云大25、云大107、PR23在我们这里种植实现一种两年四收。”防城港市农业农机服务中心推广研究员刘义明说。

收割作业完毕后，专家组现场抽取样品、当场去杂、当场称量生谷重量和测定水分含量，按《全国粮食高产创建测产验收办法》的相关要求计算干谷产量。专家一致认为：多年生稻在上思县示范推广效果明显，初步取得成功，可以在相似区域进行多年生稻推广应用。

“多年生稻早稻产量400多公斤/亩、晚稻350公斤/亩，前景相当不错。当然还有很多技术要完善，包括品种的改良以及栽培技术等。”中国水稻所研究员、专家组组长章秀福测产验收后说。



资料图片 jg'ck

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横县积极探索“多年生水稻”种植模式 一次播种可收割多年

2020-08-10 16:37



近年来，横县引进多年生水稻在陶圩镇进行试验种植，种植户只需种植一次，就可以连续收获几年，而且不需要繁琐的生产环节。近日，陶圩镇荔枝村试验种植的多年生水稻迎来收获，横县农业技术推广站对其进行了现场产量验收。

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多年生稻“云大107”在云南红河流域梯田测产验收

中国新闻网
2021-10-24 19:59:51



10月24日，当地村民将刚收割的水稻放入机器中进行初筛。当日，云南省玉溪市元江哈尼族彝族傣族自治县南洒村梯田种植的300亩多年生稻“云大107”示范区域进行了田间测产验收。



据了解，多年生稻是水稻育种的一个创新，只需栽种一次，就可连续收割两季或通过越冬后收割几年，期间不需要再购种、育秧、犁田、耙田、插秧，极大地减少了劳动力投入，降低了稻农的劳动强度，并且产量保持相对稳定，突破了传统水稻的耕作方式，实现了水稻的轻简化生产。图为当地村民扛着刚收割的一捆水稻。



多年生稻在红河流域梯田实现"一种多收"

云视新闻

2021-10-25 21:31 5,714阅读

 上七彩云端 看精彩云南

割完一季接着长，
一次栽种能连续收割多年。
在云南，有这样一种多年生稻，
可以让农民像种韭菜一样种植水稻。
目前，
多年生稻在红河流域大面积推广种植获得了成功。



10月24日，在云南省元江县南洒村梯田多年生稻“云大107”示范区，水稻测产专家组进行了田间测产验收。

中国水稻研究所研究员 章秀福：“早晚两季相加实测亩产1120.45公斤，那么这个产量已经到了比较高的水准。”

这是迄今为止多年生稻“云大107”在田间大面积种植的最高产量，标志着这一品种在红河流域梯田种植获得了成功。

那么，什么是“多年生稻”，它和我们日常食用的杂交稻有什么区别呢？

云南大学农学院教授 胡凤益：“你看它收了以后，它就从土里面再长出一个新苗来，就是割了以后不需要用种子再来繁，然后年复一年的实现了多年生。”

多年生稻在适宜区域只需种植一次，第二季起不用再经历购买种子、育秧、犁田、插秧等环节，减少了投入，减轻了田间劳动强度，种植户只需要做好田间管理就可实现连续多年的水稻轻简化生产。

其他附件

小院培养（已毕业）学生清单

学生姓名	学号	入学年份	毕业年份	学制	指导老师
施继芳	12018002396	2018	2020	二年制	胡凤益
李鹏林	12018002397	2018	2020	二年制	胡凤益
何奕霏	12018002403	2018	2020	二年制	胡凤益
李小波	12017002266	2018	2020	二年制	胡凤益
程卯	12018002411	2018	2020	二年制	张石来
刘俊雄	12018002420	2018	2020	二年制	黄立钰
王松	12018002407	2018	2020	二年制	秦世雯
何志超	12017002264	2017	2019	二年制	胡凤益
赵艳娟	12017002270	2017	2019	二年制	黄立钰
王晓光	12017002274	2017	2019	二年制	胡凤益
杨景雅	12016002220	2016	2018	二年制	黄立钰
李文飞	12016002221	2016	2018	二年制	胡凤益
章晓敏	12016002223	2016	2018	二年制	胡凤益
付玉鹏	12016002236	2016	2018	二年制	胡凤益
赵光程	12016002240	2016	2018	二年制	黄立钰
杨金玲	12016002228	2016	2018	二年制	黄立钰
敖若寅	12019101176	2019	2022	三年制	张石来
陈本佳	12019101180	2019	2022	三年制	黄立钰
杜双林	12019101181	2019	2022	三年制	张毅
李金萍	12019101182	2019	2022	三年制	李争
龚禹瑞	12019202656	2019	2022	三年制	秦世雯
管娟	12019202657	2019	2022	三年制	秦世雯
何迷	12019202658	2019	2022	三年制	黄光福
贺鸿	12019202659	2019	2022	三年制	李争
胡庆毅	12019202661	2019	2022	三年制	黄立钰
黄静	12019202663	2019	2022	三年制	张石来
李凌宏	12019202668	2019	2022	三年制	胡凤益
李翔	12019202671	2019	2022	三年制	张毅
李舟	12019202672	2019	2022	三年制	刘丹丹
刘金涛	12019202673	2019	2022	三年制	黄立钰
王坤	12019202688	2019	2022	三年制	胡凤益
周伍民	12019202708	2019	2022	三年制	黄立钰
朱文平	12019202709	2019	2022	三年制	张毅
付琦	12018001106	2018	2021	三年制	胡凤益
宁敏	12018001107	2018	2021	三年制	黄立钰
暴亚冲	12018001108	2018	2021	三年制	黄立钰
刘溥	12017001126	2017	2020	三年制	胡凤益
杨智梅	12017001128	2017	2020	三年制	胡凤益
杨洋	12016000722	2016	2019	三年制	胡凤益
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序号	科技小院	负责人
1	云南呈贡花卉科技小院	吴学蔚
2	云南临翔苹果科技小院	刘丹丹
3	云南隆阳咖啡科技小院	何飞飞
4	云南勐海多年生稻科技小院	胡凤益
5	云南呈贡工业大麻科技小院	汤开磊
6	云南富民大豆科技小院	王贤智
7	云南澄江棉花科技小院	刘海英
8	云南呈贡草莓科技小院	乔琴
9	云南嵩明马铃薯科技小院	黄斌全
10	云南嵩明大白菜科技小院	董相书