Quantitative trait loci identification for yield component traits in an Indonesian local rice variety, Untup Rajab

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Abstract. Local rice varieties often carry useful genes related to yield component traits that can be utilized to develop high-yielding rice varieties. This study aimed to identify quantitative trait loci (QTLs) for yield component traits in Untup Rajab, an Indonesian local rice variety. QTL mapping was conducted using Inclusive Composite Interval Mapping (ICIM) method on a F2 population from a cross between TN-1 and Untup Rajab, which was genotyped using SNP markers and phenotyped for several yield component traits. A total of eight QTLs were detected. Two QTLs for spikelet number per panicle were found in chromosome 6 and 9 with PVE values of 13.01% and 15.57%, respectively. Three QTLs were identified for the number of filled spikelets per panicle in chromosome 4, 6, and 12 with PVE values of 7.73%, 9.19%, and 19.51%, respectively. Two QTLs were identified for the ratio of filled spikelets to total spikelet number per panicle in chromosome 3 and 12 with PVE values of 9.73% and 10.71%, respectively, and only one QTL was identified for the number of empty spikelets per panicle in chromosome 11 with a PVE value of 11.07%. Further investigation is still needed to verify their applicability for marker-assisted rice breeding.

1. Introduction

Rice is a staple food in Indonesia and the demand for rice increases every year due to population growth [1]. In the last three years consumption of rice in Indonesia rose from 29.16, 29.48, to 29.78 million tons in 2017, 2018, and 2019 respectively. Likewise, the world rice consumption has also increased in the same period from 482.32 to 493.49 million tons [2]. The availability of rice is very important because it can affect livelihoods and economies [3], as well as food security and political stability [4]. There are some new challenges that can reduce rice production significantly such as climate change [3] and the recurrent problems of land conversion to housing, industry, and highways [4]. Developing new varieties with higher yield and better quality becomes one of the main objectives in rice breeding programs to address these situations.

Genetic variability is essential in any breeding programs to improve and produce new varieties. Indonesia has rich rice germplasm comprising local varieties and wild species that can be used as genetic resources [5]. For instance, the Indonesian Center for Agricultural Biotechnology and Genetic Resources Research and Development (ICABIOGRAD) Genebank manages 4,332 rice accessions and 3,513 of those accessions are landraces [6]. Genetic diversity study of Indonesian rice germplasm using SSR makers conducted by Thomson et al. [7] showed that traditional varieties have higher genetic variability than improved varieties. Local rice varieties that have high genetic diversity are essential resources for identifying and studying genes that control important traits, which can then be applied in new rice variety development and increase the genetic variability of elite rice varieties. For instance,
several local rice varieties have been used for developing new rice varieties those are tolerant to submergence [8], tolerant to phosphorus deficiency [9], and resistant to brown planthopper [10].

Developing new rice varieties with higher yield is one of the main objectives in breeding programs. However, it is not an easy task because multiple traits, known as yield component traits, are involved and have significant effects. Besides, yield component traits are quantitative traits controlled by several non-allelic genes [11]. Several yield component traits that determine grain yield include the number of panicles, the number of seeds per panicle, and grain weight [12,13]. Several studies have been conducted to identify genes and the location of DNA sequences related to yield traits using molecular markers [14–17]. Discovering new genes related to yield trait is always a stunning achievement and the variability of genes in local rice varieties can improve the chance of success in this effort. Untup Rajab is a local rice variety originated from Banyuwangi, East Java, Indonesia, that has QTLs for tolerance to brown planthopper [18]. Further observations showed that this variety also has a high percentage of empty seeds, thus it needs to be studied to identify the yield component traits.

The objective of this study is to identify quantitative trait loci related to yield component traits, i.e. panicles per plant, total spikelets per panicle, filled spikelets per panicle, empty spikelets per panicle, and the ratio of filled spikelets to total spikelets per panicle. The study was performed using SNP markers in a segregating F2 population developed from a cross between TN-1 and Untup Rajab.

2. Materials and Methods

2.1. Plant materials

The plant material used in this study are Untup Rajab, an Indonesian local rice variety originated from Banyuwangi, East Java, Indonesia, TN-1 and 114 individual plants from an F2 population developed from a cross between TN-1 and Untup Rajab. The population development began by sowing seeds of the two parents in water-soaked petridish layered with tissue papers and leaving them to germinate and grow for seven days. After that, the growing plants were transplanted in mud soil in a plastic box for seven days. Next, each individual plant was retransplanted to a pot filled with mud soil. The plants were watered and fertilized regularly until flowering time. Then, the plants were crossed using the TN-1 variety as the female parent and Untup Rajab as the male parent to produce F1 seeds. The F1 seeds were then grown under the same conditions as described above until flowering, and allowed to self-pollinate to produce F2 seeds. Later on, the F2 seeds were also grown in the same conditions until harvest. Leaf samples and panicles of each individual F2 plant were collected for genotyping and observing phenotypic traits related to yield components. All the procedures above were conducted in a greenhouse from August 2015 to September 2017.

2.2. Evaluation of yield component traits

Evaluation of yield component traits was conducted by observing the panicle number per plant, total spikelet number per panicle, filled spikelets per panicle, empty spikelets per panicle, and the ratio of filled spikelets to total spikelet number per panicle. Panicle number per plant was obtained by counting all panicles per individual plant. Spikelets were counted in the five first emerging panicles per plant and the results were averaged to obtain the mean numbers for a single panicle.

2.3. Genotyping F2 plants using SNP markers

Leaf samples were collected from each F2 plant and both parents for DNA isolation. The procedure for DNA isolation was conducted following the method of Dellaporta et al. [19]. The concentration of DNA samples were measured using NanoDrop™ 2000 Spectrophotometer (Thermo Scientific, USA) and dissolved to approximately 50 ng/μl for SNP analysis. Genotyping was carried out by IRRI Service Laboratories [20] using the 7K SNP BeadChip containing 7,098 bead types [21] to detect the SNP alleles in the F2 population. DNA amplification, hybridization of PCR product to the Infinium II BeadChips, staining with fluorescent dye and scanning the fluorescent intensity of the beadchip were conducted following the manufacturer’s protocol. The raw intensity data of the scanned 7K beadchip were
converted to SNP allele data using Illumina’s Genome Studio Software. Polymorphic SNP markers that segregate in the F$_2$ population were used for the genetic map construction and identification of QTLs.

2.4. Genetic map construction and identification of QTLs

The yield component data and polymorphic SNPs data were used to construct a genetic map and identify the QTLs related to panicle number per plant, total spikelet number per panicle, filled spikelets per panicle, empty spikelets per panicle, and the ratio of filled spikelets to total spikelet number per panicle. Genetic map construction and QTL identification for yield component traits were performed using QTL IciMapping software [22]. The physical location of each marker on the chromosome was added as an anchor and mapping was carried out with the following parameter settings: Kosambi mapping function, grouping with LOD 3.0, ordering with the nearest neighbor two-opt (nnTwoOpt), and rippling with sum of adjacent recombination fractions (SARF) and window size = 5. QTL identification was performed using Inclusive Composite Interval Mapping (ICIM-ADD) with the following parameters: delete missing data, scanning step 1 cM, probability in stepwise regression (PIN) 0001, and logarithm of the odds (LOD) threshold 2.5.

3. Results and Discussions

Genotypic and phenotypic data for panicle number per plant were obtained from 114 individual plants. However, the data for other traits could only be collected from 103 individual plants because some of the data were missing. The performance of three F$_2$ plants and the parents used in this study are shown in Figure 1.

![Figure 1. The performance of three F$_2$ plants and both parents (TN-1 and Untup Rajab).](image-url)

The phenotypic data had relatively normal distribution except for empty spikelets per panicle and the ratio of filled spikelets to total spikelet per panicle, which were relatively skewed and needed to be transformed into logarithmic and arcsin form, respectively. The genetic linkage map was constructed using 885 polymorphic markers out of the 7,098 total SNP makers found in the chip. These polymorphic markers were well-distributed in 12 rice chromosomes with 73 markers in average per chromosome. The total length of the genetic map was 4136.09 cM with an average distance between markers of 4.6 cM.
Figure 2. Chromosomal location of QTLs for total spikelet per panicle, filled spikelet per panicle, the ratio of filled spikelet to total spikelet per panicle, and empty spikelets per panicle, identified using SNP markers in a F$_2$ population from a cross between TN-1 and Untup Rajab varieties.

QTLs were detected for all traits except for the panicle number per plant, as shown in Figure 2 and Table 1. Two QTLs were identified for spikelet number per panicle in chromosome 6 and 9. The QTL in chromosome 6 was located between 300.06–304.04 cM positions in the genetic map, between bases 27,609,766–27,900,452 in the physical map, flanked by markers 6855107 and 6864051, with a LOD score of 2.64, and PVE value of 13.01%. Meanwhile, the QTL in chromosome 9 was mapped between 43.63–47.16 cM positions in the genetic map, between bases 9,324,647–9,945,590, flanked by marker 9447279 and 9471936, with a LOD score of 2.80 and PVE value of 15.57%. Several previous studies
have identified one QTL related to spikelet number per panicle in chromosome 4 [23], chromosome 5 [24], chromosome 6 [16], and chromosome 12 [25]. Sasaki et al. [17] used two different crosses and identified two loci related to spikelet number per panicle in chromosome 12. Furthermore, Jia et al. [26] found two loci linked to spikelet number in chromosome 6 and chromosome 12. Genes and QTLs, which were also identified in the same segment previously, were also searched in the Gene Browser of Q-TARO database [27]. Q-TARO reported the presence of QTLs in chromosome 6 at base position 27,288,493–29,906,021 and 10,015,514–28,130,383, that were related to panicle number [28] and weight of 1000 grains [29]. Besides, one QTL that was identified in chromosome 9 at base position 9,783,058–9,783,612 was related to dense panicle [30].

Two previous studies have identified QTLs for spikelet number per panicle in chromosome 6. The first one is the study by Jia et al. [26] that found 2 QTLs in this chromosome with PVE values of 10.0% and 12.3%, a little lower than the values obtained in this study. The second one was the study conducted by Kim et al. [16], but it did not inform the PVE value. However, there were no QTL detected in chromosome 9 for this trait in all of the surveyed literatures. Therefore, the QTL for spikelet number detected in this study could be a novel gene that controls the trait. Q-TARO also documented QTLs for spikelet number in chromosome 6 and 9. However, the QTL in chromosome 6 is related to a different trait, while the QTL in chromosome 9 was for dense panicle, which could be an alternative way in describing the number spikelet per panicle.

QTLs for filled spikelet number were identified in chromosome 4, 6, and 12. The QTL in chromosome 4 was located between 79.73–82.39 cM in the genetic map, between bases 31,509,862 and 31,678,446, between flanking markers 4704444 and 4711121, with a LOD score of 2.86, and PVE value of 7.73%. Chromosome 6 has QTL that located between 37.60–65.38 cM in the genetic map, from bases 2,130,188 to 3,154,729, flanked by markers 5883472 and id6002535, with a LOD score of 2.59 and PVE value of 9.19%. The QTL in chromosome 12 was located between 29.23–58.21 cM in the genetic map, between bases 21,222,251 and 18,445,418, between flanking markers SNP-12.2118879 and id12006190, with a LOD score of 4.47 and PVE value of 19.51%. Marathi et al. [15] identified seven QTLs related to the filled grain in chromosome 2, 3, 4, 7, and 12, where each chromosome contained 1, 2, 2, 1, and 1 QTLs, respectively, with PVE values that ranged between 12%–22%. Rabiei et al. [25] mapped QTLs for filled grain per panicle in chromosome 1, 6 and 11. The QTL they found in chromosome 6 had 2.13% of PVE value, lower than the 9.19% value observed in this study. Jia et al. [26] identified three QTLs for filled grain number in chromosome 8, 11, and 12. The Q-TARO database reported one gene and one QTL in chromosome 4 between the base position 31,610,701 to 31,613,275 and between bases 31,648,882 to 32,036,068, which are related to grain number per panicle [31] and sink capacity [32], respectively. Q-TARO also documented one QTL in chromosome 12 at base position 5,820,051 to 24,012,742, which is related to 1000 grain weight trait [33]. No QTL information associated with filled spikelet number was found in chromosome 6 in Q-TARO database.

QTLs were also identified when the trait was scored as the ratio of filled spikelet number to total spikelet number per panicle. Two QTLs related to this trait were identified in chromosome 3 and 12. The QTL in chromosome 3 was located between 189.22–245.15 cM in the genetic map, between bases 10,798,981 to 14,652,095, flanked by markers 2739775 and 2853978, with a LOD score of 3.27 and PVE value of 9.73%. The other QTL in chromosome 12 was located between 29.23–58.21 cM in the genetic map, between bases 21,222,251 and 18,445,418, between flanking markers SNP-12.2118879 and id12006190, with a LOD score of 4.24 and PVE value of 10.71%. The QTL for the filled spikelet ratio in chromosome 12 overlapped with the QTL for filled spikelet number per panicle. Q-TARO database showed that one QTL related to grain yield existed in chromosome 3 at the base position 9,015,683 to 12,199,844, while in chromosome 12 one QTL existed at base position 5,820,051–24,012,742, although this QTL is related to 1000 grain weight [33] instead of the ratio of filled spikelet number to total spikelet number per panicle.
Two QTLs were identified to be applied, which demonstrated that the utility of identified QTLs in the previous studies might have small allelic effects on the phenotype and normal distribution. Nonetheless, some QTLs that have reasonably high PVE values could be utilized for rice breeding programs to increase productivity. Rabiei et al. [25] considered QTLs with PVE value of 15.23% as a major effective QTL. Therefore, the QTL for filled spikelet number with 19.91% PVE value has a potential to be applied in marker-assisted breeding to improve the productivity of rice varieties.

QTL for empty spikelets was only identified in chromosome 11. It is located between 296.55–297.42 cM in the genetic map, between bases 28,739,517 and 28,778,673, flanked by markers 11992907 and SNP-11.28255452, with a LOD score of 2.58 and PVE value of 11.07%. Previous study by Rabiei et al. [25] mapped 3 QTLs related to empty spikelets in chromosome 2, 3, and 12, whereas Marathi et al. [15] identified two QTLs related to percent sterility in chromosome 3 and 11 but they did not report the PVE values for those QTLs. The Q-TARO database has one QTL in chromosome 11 at base position 24,948,460 to 28,848,614, but it is related to floral organ number [34].

In general, this study obtained relatively low PVE values for yield component traits, which ranged from 7.73 to 19.91% in all chromosomes. The phenotype data of each yield component trait have relatively normal distribution, except for some data that had to be transformed into other forms. These results confirmed that the traits are quantitative in nature. Mackay [35] indicated that quantitative traits have small allelic effects on the phenotype and normal distribution. Nonetheless, some QTLs that have reasonably high PVE values could be utilized for rice breeding programs to increase productivity. Rabiei et al. [25] considered QTLs with PVE value of 15.23% as a major effective QTL. Therefore, the QTL for filled spikelet number with 19.91% PVE value has a potential to be applied in marker-assisted breeding to improve the productivity of rice varieties.

The molecular markers used in this study were SNP markers while most previous studies used SSR markers to detect the QTLs. Therefore, the QTLs that were detected in the same chromosomes as the QTLs in the previous studies might need to be investigated further to ascertain whether the QTLs have the same genetic basis or only occurred to be located in the same chromosomal regions by chance, but have completely different genetic mechanisms. In order to achieve this purpose, these two marker types should be merged into the same genetic map. This has been applied in the construction of high resolution linkage maps of soybean, which was constructed by incorporating different types of markers into one linkage map [36]. In addition, further studies are still needed to confirm the utility of identified QTLs with high PVE values and demonstrate that the new candidate QTLs would help improve rice varieties with high yield.

4. Conclusions
A total of eight QTLs were detected for all traits except for the number of panicles. Two QTLs were identified for the number spikelet per panicle in chromosome 6 and 9. Three QTLs were identified for the number of filled spikelet per panicle in chromosome 4, 6, and 12. Two QTLs were identified for the

**Table 1. QTLs for total spikelets per panicle (TS), filled spikelets per panicle (FS), ratio of filled spikelets to total spikelet per panicle (F/T), and empty spikelets per panicle (ES), identified using SNP markers in a F2 population from a cross between TN-1 and Untup Rajab varieties.**

| Traits | Chr | Position (cM) | Position (Base pair) | Left marker | Right marker | LOD | PVE(%) | Add | Dom |
|--------|-----|---------------|----------------------|-------------|--------------|-----|--------|-----|-----|
| TS     | 6   | 300.06-304.04 | 27609766-27900452    | 6855107     | 6864051      | 2.65 | 13.01  | 12.04 | -11.52 |
|        | 9   | 43.63-47.16   | 9324647-9945590      | 9447279     | 9471936      | 2.80 | 15.57  | -14.67 | 2.27  |
| FS     | 4   | 79.73-82.39   | 31509862-31678446    | 4704444     | 4711121      | 2.86 | 7.73   | -14.99 | 0.02  |
|        | 6   | 37.6-65.38    | 2130188-3154729      | 5883472     | id6002535    | 2.59 | 9.19   | 13.60 | 12.42 |
|        | 12  | 29.23-58.21   | 21222251-18445418    | SNP-12.21188797. | id12006190 | 4.47 | 19.51  | -25.71 | 11.70 |
| F/T    | 3   | 189.22-245.15 | 1079891-14652095     | 2739775     | 2853978      | 3.27 | 9.73   | -0.19  | 0.17  |
|        | 12  | 29.23-58.21   | 21222251-18445418    | SNP-12.21188797. | id12006190 | 4.24 | 10.71  | -0.18  | 0.17  |
| ES     | 11  | 296.55-297.42 | 28739517-28778673    | 11992907    | SNP-11.28255452. | 2.58 | 11.07  | -0.11  | 0.07  |

Chr = chromosome, LOD = logarithm of the odds, PVE = phenotypic variation explained, Add = additive effect of allele substitution, Dom = dominant effect of allele substitution, TS = total spikelets, FS = filled spikelets, F/T = ratio of filled spikelets to total spikelets, ES = empty spikelets.
ratio of a filled spikelet to total spikelet number per panicle in chromosome 3 and 12. In contrast, one QTL was identified for the number of empty spikelets per panicle in chromosome 11.

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References

[1] Arifin B, Achsani N A, Martianto D, Sari L K and Firdaus A H 2019 J. Ekon. Indones. 8 71–102
[2] Fusat Data dan Sistem Informasi Pertanian 2019 Bul. Konsumsi Pangan 10 11–21
[3] Redfern S K, Azza N and Binamira J S 2012 Proc. Joint FAO/OECD Works. on Building Resilience for Adaptation to Climate Change in the Agriculture Sector 23–24 April 2012 Rome (Rome: FAO) pp 295–314
[4] Khush G S 2013 Plant Breed. 132 433–6
[5] Sitaresmi T, Wening R H, Rakhmi A T, Yunani N and Susanto U 2015 Iptek Tanam. Pangan 8 22–30
[6] Sabran M, Hidayatun N and Kurniawan H 2020 Digital Object Identifiers for Indonesia Rice Germplasm Boosting the Big Data of Plant with Digital Identifiers ed M Sabran et al (Jakarta: IAARD Press) chapter 5 pp 328–45
[7] Thomson M J, Septiningsih E M, Suwardjo F, Santoso T J, Silitonga T S and McCouch S R 2007 Theor. Appl. Genet. 114 559–68
[8] Septiningsih E M, Pamplona A M, Sanchez D L, Neeraja C N, Vergara G V, Heuer S, Ismail A M and Mackill D J 2009 Ann. Bot. 103 151–60
[9] Chin J H, Gamuyao R, Dalid C, Bustamam M, Prasetiyono J, Moeljopawiro S, Wissuwa M and Heuer S 2011 Plant Physiol. 156 1202–16
[10] Sansanoh R, Sreewongchay T, Chansri R, Kongsil P and Wangsawang T 2019 Agric. Nat. Resour. 53 38–43
[11] Zhou S, Zhu M, Wang F, Huang J and Wang G 2013 Pakistan J. Bot. 45 183–9
[12] Liu E, Zeng S, Chen X, Dang X, Liang L, Wang H, Dong Z, Liu Y and Hong H 2017 Identification of putative markers linked to grain plumpness in rice (Oryza sativa L.) via association mapping. BMC Genet. (2017) 18 89
[13] Xu F, Jin L, Huang Y, Tong C, Chen Y L and Bao J S 2016 J. Integr. Agric. 15 2192–202
[14] Fung Y, Zhai R R, Lin Z C, Cao L Y, Wei X H and Cheng S H 2015 Rice Sci. 22 108–15
[15] Marathi B, Guleria S, Mohapatra T, Parsad R, Mariappan N, Kurungara V K, Atwal S S, Prabhu K V, Singh N K and Singh A K 2012 QTL analysis of novel genomic regions associated with yield and yield related traits in new plant type based recombinant inbred lines of rice (Oryza sativa L.). BMC Plant Biol. (2012) 12 137
[16] Kim D M, Lee H S, Kwon S J, Fabreag M E, Kang J W, Yun Y T, Chung C T and Ahn S N 2014 Rice 7 1–11
[17] Sasaki K, Fujita D, Koide Y, Lumanglas P D, Gannaban R B, Tagle A G, Obara M, Fukuta Y, Kobayashi N and Ishimaru T 2017 J. Exp. Bot. 68 2693–702
[18] Yunus M, Damayanti D, Dadang A, Warsun A, Satyawan D, Kusumanegara K, Dewi I S, Sutrisno S and Husin B A 2018 J. AgroBiogen 14 75 – 84
[19] DellaPorta S L, Wood J and Hicks J B 1983 Plant Mol. Biol. Report. 1 19–21
[20] IRRI Service Laboratories Retrieved from https://gsl.irri.org/services/genotyping/7k
[21] Morales K Y, Singh N, Perez F A, Ignacio J C, Thapa R, Arbelaez J D, Tabien R E, Famoso A, Wang D R, Septiningsih E M, Shi Y, Kretzschmar T, McCouch S R and Thomson M J 2020
An improved 7K SNP array, the C7AIR, provides a wealth of validated SNP markers for rice breeding and genetics studies PLoS One (2020) 15 e0232479

[22] Meng L, Li H, Zhang L and Wang J 2015 Crop J. 3 269–83
[23] Fujita D, Tagle A G, Ebron L A, Fukuta Y and Kobayashi N 2012 Breed. Sci. 62 18–26
[24] Luo X, Ji S D, Yuan P R, Lee H S, Kim D M, Balkunde S, Kang J W and Ahn S N 2013 Rice 6 1–10
[25] Rabiei B, Kordrostami M, Sabouri A and Sabouri H 2015 Agric. Conspec. Sci. 80 91–99
[26] Jia B, Zhao X, Qin Y, Irfan M, Kim T H, Wang B, Wang S and Sohn J K 2019 Mol. Biol. Res. Commun. 8 9–15
[27] Q-TARO (QTL Annotation Rice Online) database Retrieved from http//qtaro.abr.affrc.go.jp
[28] Zhuang J Y, Fan Y Y, Wu J L, Xia Y W and Zheng K L 2001 Yi Chuan Xue Bao 28 458–64
[29] Cho Y G, Kang H J, Lee J S, Lee Y T, Lim S J, Gauch H, Eun M Y and McCouch S R 2007 Crop Sci. 47 2403–17
[30] Yu Z H, Kinoshita T, Sato S and D T S 1992 Rice Genet. Newsl. 9 116–8
[31] Zhang G-H, Li S-Y, Wang L, Ye W-J, Zeng D-L, Rao Y-C, Peng Y-L, Hu J, Yang Y-L, Xu J, Ren D-Y, Gao Z-Y, Zhu L, Dong G, Hu X-M, Yan M-X, Guo L-B, Li C-Y and Qian Q 2014 Mol. Plant 7 1350–64
[32] Mao B, Cai W J, Zhang Z H, Hu Z L, Li P, Zhu L H and Zhu Y G 2003 Yi Chuan Xue Bao 30 1118–26
[33] Zhuang J Y, Fan Y Y, Wu J L, Xia YW and Zheng K L 2000 Rice Genet. Newsl. 17 49–51
[34] Jiang L, Zhang W, Xia Z, Jiang G, Qian Q, Li A, Cheng Z, Zhu L, Mao L and Zhai W 2007 Mol. Genet. Genomics 277 263–72
[35] Mackay T F C 2009 Q&A: Genetic analysis of quantitative traits J. Biol. (2009) 8 23
[36] Song Q, Jenkins J, Jia G, Hyten D L, Pantalone V, Jackson S A, Schmutz J and Cregan P B 2016 Construction of high resolution genetic linkage maps to improve the soybean genome sequence assembly Glyma1.01 BMC Genomics (2016) 17 33