Two Useful Semidwarfing Genes in a Short-culm Mutant line HS90 of Rice (Oryza sativa L.)

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Summary
A short-culm mutant line HS90, which was induced from a Japanese rice variety Gimbozu by gamma-ray irradiation, was analyzed for the genetic factors controlling its short culmness. Compared with the original variety, HS90 has about 35 \% reduced culm length and flowers later by a few days. The F\textsubscript{1}, F\textsubscript{2} and F\textsubscript{3} generations of four crosses, Gimbozu \times HS90, Jukkoku \times Shiranui, HS90 \times Jukkoku and Gimbozu \times Jukkoku, were grown in a paddy field for genetic analysis. A variety Shiranui has already been proved to harbor a semidwarfing gene \textit{sd-1}, while Jukkoku so far has been assumed to harbor \textit{sd-1} because of the cross parent of the former. In each cross, several F\textsubscript{1} plants, about 300 F\textsubscript{2} plants, and 50 to 90 F\textsubscript{3} lines which were raised from randomly selected F\textsubscript{2} plants were examined for culm length and heading date. It was clarified that the shortening of HS90 is caused by an induced mutant semidwarfing gene (tentatively \textit{sd-1}\textsuperscript{D}), an incomplete recessive gene identical with or allelic to \textit{sd-1}. This mutant semidwarfing gene causes remarkable reduction of culm length (ca. 35 \%): its genotypic value in the heterozygous state seems almost equal to that of the midparent. In addition, HS90 was proved to harbor another incomplete recessive semidwarfing gene (tentatively \textit{sd(t)}) non-allelic to \textit{sd-1}, which was derived from the original variety Gimbozu. This semidwarfing gene reduces culm length less than \textit{sd-1}\textsuperscript{D} (ca. 20 \%): its genotypic value in the heterozygous state seemed somewhat larger than that of the midparent. As Gimbozu and its derivative varieties have often been used as a cross parent in Japanese rice breeding, the semidwarfing gene \textit{sd(t)} seemed to be widely distributed among Japanese rice varieties. The F\textsubscript{1} plants of HS90 (\textit{sd-1}\textsuperscript{D} \textit{sd-1}\textsuperscript{D} \textit{sd(t)} \textit{sd(t)} \textit{sd(t)}) \times Gimbozu (\textit{sd-1} \textit{sd-1} \textit{sd(t)} \textit{sd(t)} \textit{sd(t)}) exhibited a culm length coming within the category of semidwarfism optimum for the present cultivation methods; hence, the genotype of the F\textsubscript{1} plants, \textit{sd-1} \textit{sd-1}\textsuperscript{D} \textit{sd(t)} \textit{sd(t)}, was considered favorable for \textit{F\textsubscript{1}} hybrid rice varieties. In this study, it was also verified that the genotype of major-genes controlling the culm length of Jukkoku is identical with that of Shiranui, which indicates that Shiranui inherited \textit{sd-1} from Jukkoku.

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Key Words: Oryza sativa, mutation, semidwarfing gene, gene analysis, culm length.

Introduction
The release of semidwarf rice varieties with stiff-culm has made it possible to apply high-yielding cultivation techniques such as heavy input of chemical fertilizers and dense planting; the productivity and stability in rice cultivation have remarkably increased throughout the world. According to some recent reports, however, the existing semidwarfing gene resource base is quite smaller than expected, and the semidwarfism of most of the semidwarf varieties cultivated today is controlled by a single semidwarfing gene at \textit{sd-1} locus (Aquino and Jennings 1966, Futsuhara 1968, Seetharaman and Srivastava 1969, Foster and Rutger 1978, Chang et al. 1984, Kikuchi et al. 1985, Oba et al. 1990). Such a situation is far from the idea that the genetic diversity should be maintained, and suggests that exploiting new useful semidwarfing genes is of urgent necessity.

From a point of view that the utilization of artificially induced mutation is one of the effective methods in exploiting new semidwarfing genes (Hu 1973, Rutger et al. 1976, Mackill and Rutger 1979, Rutger 1983, Yamagata et al. 1982, Yamagata et al. 1988, Tanisaka et al. 1990), the authors have been engaged in the works on inducing and collecting a lot of short-culm mutants, and have analyzed the inheritance of their short-culmness. We have already detected a useful semidwarfing gene \textit{d-60} in a mutant breeding line Hokuriku 100 which was induced from a rice variety Kosshihikari (Tanisaka et al. 1990). This paper discusses the two useful semidwarfing genes detected in a short-culm mutant line HS90 which was artificially induced from a Japanese rice variety Gimbozu.

Materials and Methods
A short-culm mutant line HS90, which was induced with gamma-ray irradiation to the seeds of a rice variety Gimbozu, was analyzed for the genetic factors controlling its short-culmness. Compared with the original vari-
etly, HS90 has about 35% reduced culm length and flowers later by a few days (Fig. 1, Table 1). Excepting these two traits, this mutant line appears not to have any mutations.

In the analysis, three varieties, Gimbozu, Jukkoku, and Shiranui, were used along with HS90. Gimbozu, which had been cultivated mainly in the Hokuriku district in Japan till 1940s, has a comparatively short culm for a former variety, and was used as a test variety to analyze the mutant gene(s) in HS90. Both Jukkoku and Shiranui are representative semidwarf varieties which had been cultivated mainly in the Kyusyu district in Japan till lately: the latter is an improved variety harboring sd-1 (Kikuchi et al. 1985), while the former is an indigenous variety which so far has been assumed to harbor sd-1 in that it was the cross parent of the latter. Jukkoku was used as a test variety to analyze the allelic relationship of the mutant gene in HS90 to sd-1, for in this study it was proved to harbor sd-1. The culm lengths and heading dates of HS90 and the three varieties were shown in Table 1.

The F1, F2, and F3 generations of 4 crosses, Gimbozu × HS90, Jukkoku × Shiranui, HS90 × Jukkoku and Gimbozu × Jukkoku, were submitted to gene analysis for culm length. In each cross, about 5 F1 plants, about 300 F2 plants, and 50 to 90 F3 lines (ca. 25 plants/line) were used. Each F3 line was the progeny of the F2 plant randomly selected out of all the F2 plants. These materials were grown in a paddy field in Kyoto together with their cross parents and measured for culm length and heading date. The experiments were made from 1988 to 1992. In all the years, seedling and transplanting were made in the middle of May and at the end of June, respectively. Fertilizers applied were 6, 9 and 9 kg/10a for N, P2O5 and K2O, respectively, and plant spacing was 10×30 cm.

In the F2 and F3 of one of the 4 crosses, Gimbozu × Jukkoku, there was observed a comparatively large variation for heading date. Generally in rice, culm length is positively correlated with days from seedling to heading (Vergara et al. 1965, Tanisaka et al. 1989); the segregation analysis for culm length with this cross was carried out in consideration of the correlation of culm length with heading date.

Results

Gimbozu × HS90

First, the induced mutant gene(s) responsible for the shortening of HS90 was examined through the segregation analysis for culm length in the F1, F2 and F3 of Gimbozu × HS90. Fig. 2 shows the frequency distribution of culm length of the F2 plants as well as the mean culm length of the F1 plants.

The F1 plants exhibited a culm length nearly equal to the midparent value, and the F2 population showed a trimodal frequency distribution of culm length without any transgressive segregants, suggesting a 1:2:1 segregation for HS90-type : F1-type : Gimbozu-type plants. From these facts, it was inferred that the shortening of HS90 is caused by one induced mutant semidwarfing gene, which acts as an incomplete recessive or dominant gene bringing about a remarkable reduction of culm length, and of which genotypic value in the heterozygous state is nearly equal to that of the midparent.

The F3 progeny test was made to confirm this point.

![Fig. 1. A short-culm mutant line HS90 (right), its original variety Gimbozu (left) and the F1-type plant between them (middle).](image)

![Fig. 2. Frequency distribution of culm length in F3 (Gimbozu × HS90).](image)

<table>
<thead>
<tr>
<th>Variety or line</th>
<th>Culm length (cm)</th>
<th>Heading date</th>
</tr>
</thead>
<tbody>
<tr>
<td>HS90</td>
<td>52</td>
<td>Sep. 3</td>
</tr>
<tr>
<td>Gimbozu</td>
<td>81</td>
<td>Sep. 3</td>
</tr>
<tr>
<td>Shiranui</td>
<td>61</td>
<td>Sep. 7</td>
</tr>
<tr>
<td>Jukkoku</td>
<td>72</td>
<td>Sep. 7</td>
</tr>
</tbody>
</table>

Table 2 illustrates the three types of frequency distribution within F₃ line corresponding to the genotypes and phenotypes of the parental F₂ plants. As clearly seen from the table, all the 50 F₃ lines could easily be classified into three groups. The ratio of 10:27:13 for [recessive-homozygous, HS90-type]: [heterozygous, F₁-type]: [dominant-homozygous, Gimbozu-type] lines fitted to a 1:2:1 expected for one-gene segregation ($\chi^2 = 0.680$, 0.500 $< P < 0.750$). In addition, the heterozygous plants, i.e., the F₁-type plants, tended to have a little longer culm length than the midparent.

The results of the F₃ progeny test show the accuracy of the above inference about the induced semidwarfing gene in HS90, and indicate that this mutant gene acts as an incomplete recessive gene.

**Jukkoku × Shiranui**

Jukkoku so far has been assumed to be a sd-l donor of Shiranui by several researchers (Kikuchi et al. 1985 etc.), but the accuracy of this assumption has not been experimentally verified yet. Before using Jukkoku as a test variety with sd-l, we investigated the accuracy of the assumption through the segregation analysis for culm length in the progenies of Jukkoku × Shiranui.

As seen from Fig. 3, the F₁ plants exhibited a culm length nearly equal to the midparent value, and the F₂ population showed a unimodal frequency distribution of culm length without any transgressive segregants. In addition, the variation of culm length within F₂ population was so small. From these facts, it was inferred that the genotype of major-gene(s) controlling the culm length of Jukkoku is identical with that of Shiranui, and the small difference in culm length between the two varieties is ascribable to the effects of minor-genes.

The results of the F₃ progeny test were given in Table 3. The variation of culm length among lines was so small, and no transgressive lines appeared in either direction. In addition, the mean culm length of the shortest line was well consistent with that of the shorter-culm parent, while the mean culm length of the longest line was well consistent with that of the longer-culm parent. On the other hand, as for the within-line-variation of culm length, there were not found any significant differences among the lines inclusive of the parent ones.

These results indicate that Jukkoku and Shiranui have the same genotype for major-gene(s) controlling culm length, that is, Jukkoku harbors sd-I; hence, it can safely be said that Shiranui inherited sd-I from Jukkoku.
HS90 × Jukkoku
The allelic relationship of the induced mutant semi-
dwarfing gene in HS90 to sd-1 was investigated through
the segregation analysis for culm length in the pro-
genies of HS90 × Jukkoku. Fig. 4 shows the frequency
distribution of culm length of the F₂ plants as well as
the mean culm length of the F₁ plants. In the F₂, there
was observed a unimodal frequency distribution without
any transgressive segregants. However, the F₁ plants
exhibited a culm length somewhat longer than the
midparent value, and the variation of culm length within
F₂ population was not so small as to be ascribable to
the effects of minor-genes; hence, it was inferred that
the variation of culm length resulted mainly from the
segregation of major-gene(s), though the number of seg-
regating genes could not be estimated.

As illustrated in Table 4, all the 50 F₃ lines were
easily classified into three groups corresponding to
the genotypes and phenotypes of the F₂ parental plants. The
ratio of 12 : 22 : 16 for [recessive-homozygous,
HS90-type] : [heterozygous, F₁-type] : [dominant-
homozygous, Jukkoku-type] lines fitted to a 1 : 2 : 1 ex-
pected for one-gene segregation (χ²=1.36, 0.500<P<
0.750).

These results indicate that HS90 harbors one incom-
plete recessive semidwarfing gene that Jukkoku does
not harbor, but it is yet to be seen whether the induced
mutant gene in HS90 is allelic to sd-1 or not.

Gimbozu × Jukkoku
If the number of segregating genes in the F₂ of Gimbozu
× Jukkoku is known, the allelic relationship between the
induced mutant semidwarfing gene in HS90 and sd-1 will
be clear, because the number of segregating genes in the
F₂ of the two crosses, HS90 × Gimbozu and HS90 × Juk-
koku, have already been clarified. Fig. 5 shows the scatter
diagram of days to heading and culm length of the F₂ plants
derived from Gimbozu × Jukkoku. As seen from this figure,
the variation of days to heading, ranging from 98 to 133,
was so large that the segregation

<table>
<thead>
<tr>
<th>Table 3. Frequency distribution of culm length in some of F₃ lines (Jukkoku × Shiranui)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean for</td>
</tr>
<tr>
<td>-----------------------------------------------</td>
</tr>
<tr>
<td>culm length</td>
</tr>
<tr>
<td>shortest</td>
</tr>
<tr>
<td>middle</td>
</tr>
<tr>
<td>tallest</td>
</tr>
<tr>
<td>Shiranui</td>
</tr>
<tr>
<td>Jukkoku</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table 4. Classification of F₃ lines based on the segregation type of culm length (HS90 × Jukkoku)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frequency distributions of culm length in representative F₃ lines</td>
</tr>
<tr>
<td>No. of F₃ lines</td>
</tr>
<tr>
<td>Phenotype and genotype</td>
</tr>
<tr>
<td>------------------------</td>
</tr>
<tr>
<td>HS90 type</td>
</tr>
<tr>
<td>recessive homozygous</td>
</tr>
<tr>
<td>F₁ type</td>
</tr>
<tr>
<td>heterozygous</td>
</tr>
<tr>
<td>Jukkoku type</td>
</tr>
<tr>
<td>dominant homozygous</td>
</tr>
<tr>
<td>HS90</td>
</tr>
<tr>
<td>Jukkoku</td>
</tr>
</tbody>
</table>

(Test for one-gene segregation: χ²=1.360, 0.500<P<0.750)
Two useful semidwarfing genes in a mutant line of rice

analysis in this cross was carried out in consideration of the correlation of culm length with heading date.

Excepting the effect of days to heading on culm length, the F₁ plants was presumed to exhibit a culm length nearly equal to the midparent value, and in the F₂, distinct transgressive-segregants for culm length appeared in both directions at any heading date. This suggested that the segregation of culm length in the F₂ of this cross resulted mainly from the segregation of more than two major-genes, and one parent harbors at least one semidwarfing gene that the other parent does not harbor.

As illustrated in Table 5, all the F₃ lines were classified into 9 groups corresponding to the genotypes and phenotypes of the F₂ parental plants, suggesting that two semidwarfing genes segregated independently. In Table 5, the semidwarfing gene in Gimbozu and that in Jukkoku are tentatively designated as a and b, respectively. The ratio of 6 : 12 : 5 : 10 : 17 : 7 : 9 : 18 : 6 for [aabb, transgressively short] : [AAbb, transgressively short] : [AAbb, Jukkoku-type] : [aaBb, slightly shorter than F₁-type] : [AAbb, F₁-type] : [AAbb, slightly shorter than Gimbozu-type] : [aAbB, Gimbozu-type] : [AAbb, transgressively long] : [AAbb, transgressively long] lines fitted to a 1 : 2 : 1 : 2 : 4 : 2 : 1 : 2 : 1 expected for two-gene segregation (χ²=9.333, 0.250<P<0.500). In addition, all the F₃ lines derived from aabb plants showed a mean culm length consistent with that of HS90.

These results indicate that Gimbozu harbors one semidwarfing gene, a, non-allelic to sd-1, and the one-gene segregation observed in the F₂ of HS90×Jukkoku resulted mainly from the segregation of a locus.

Consequently, it can be concluded that HS90 harbors two semidwarfing genes: one is an induced mutant gene identical or allelic to sd-1 in Jukkoku and the other is an existing gene derived from the original variety Gimbozu.

Discussion

Experiment results show that HS90 harbors two semidwarfing genes: one is a semidwarfing gene induced in Gimbozu and allelic to sd-1, and the other is a semidwarfing gene derived from Gimbozu and non-allelic to sd-1. For the convenience of description, the induced semidwarfing gene and the semidwarfing gene derived from Gimbozu are tentatively designated as sd-Ia and sd(t), respectively.

Table 5. Classification of F₃ lines based on the segregation type of culm length (Gimbozu×Jukkoku)

<table>
<thead>
<tr>
<th>Phenotype and genotype</th>
<th>Frequency distributions of culm length in representative F₂ lines</th>
<th>No. of F₂ lines</th>
<th>Observed</th>
<th>Expected</th>
</tr>
</thead>
<tbody>
<tr>
<td>of F₂ plant</td>
<td>50      60 70 80 90                       100 110(cm)</td>
<td></td>
<td>5.625</td>
<td></td>
</tr>
<tr>
<td>Transgressively short</td>
<td>aabb</td>
<td>3 7 3 2 5 2</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>AAbb</td>
<td>1 2 2 2 3 3 5 2 1 1</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Jukkoku type</td>
<td>AAbb</td>
<td>1 1 4 4 1 3 6 3</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Slightly shorter than F₁ type</td>
<td>aabb</td>
<td>2 1 1 1 1 1 3 3 3 2 2 1 1 2</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>F₁ type</td>
<td>AAbb</td>
<td>1 2 2 1 1 1 1 2 3 1 2 2</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>Slightly shorter than Gimbozu type</td>
<td>AAbb</td>
<td>1 3 1 4 4 1 1 1 2 2 1 1</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Gimbozu type</td>
<td>aabbB</td>
<td>1 7 5 3 4 2 1</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Transgressively long</td>
<td>AAbb</td>
<td>1 1 1 1 1 5 1 4 2 1 3 1</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>AAbb</td>
<td>1 1 3 2 3 3 2 4 1</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>

Jukkoku (AAbb)                      1 1 5 8 15 7 7 2
Gimbozu (aabbB)                     3 5 7 5 10 9 2 6 1
HS90 (aabb)                         2 6 9 12 11 5 1

(For use-one gene segregation: χ²=9.333, 0.250<P<0.500)

1) a, A : Semidwarfting gene of Gimbozu and its allele, respectively.
2) b, B : Semidwarfing gene of Jukkoku and its allele, respectively.
3) All the F₃ lines presented here showed a narrow variation for heading date ranging from Gimbozu-type to Jukkoku-type.
In addition to ours, there are several reports indicating the success of artificial induction of mutant semidwarfing gene at sd-1 locus (Foster and Rutger 1978, Mackill and Rutger 1979, Carnahan et al. 1981, Rutger et al. 1976, Futsuhara 1968): these genes were induced separately in different varieties and most of them so far have been used directly or indirectly in practical semidwarf rice breeding. It has not been clarified yet whether these genes are identical with each other or not, but it is noted that all of these genes were induced by gamma-ray irradiation. There is plenty of evidence that the spectrum of induced mutations is not alike if different mutagens are applied (Ehrenberg et al. 1956, Nybom 1956, Hagberg et al. 1958, Gustafsson 1961, Nilan 1972, Auerbach 1976, Tanisaka and Yamagata 1984). For the lack of information about the other mutagens, it is not apparent whether sd-1 locus specifically reacts to gamma-rays or not, but it can at least be said that the application of gamma-rays is useful for the induction of mutant semidwarfing genes at sd-1 locus.

The difference in culm length between HS90 and its original variety Gimbozu reflects the effect of sd-1b, because the genetic background of HS90 does not differ much from that of Gimbozu. Therefore, it is reasonable to estimate that sd-1b reduces culm length by ca. 35% in the homozygous state (Table 1). On the other hand, the F3 lines derived from the F2 plants harboring both sd-1 from Jukkoku and sd(t) from Gimbozu in the homozygous state exhibited a culm length nearly equal to that of HS90 (genotype : sd-1b sd-1b sd(t) sd(t)) (Table 5). This suggests that the sd-1 in Jukkoku (tentatively designated as sd-1p) has almost the same effect on culm length as sd-1b, reducing culm length by ca. 35%. According to Kikuchi et al. (1985), the sd-1 in Shiranui, i.e. sd-1p (Fig. 3, Table 3), reduces culm length by ca. 30%. The difference (ca. 5%) in culm length reduction effect of sd-1p must be attributable to the differences in genetic background and/or growing condition. On the contrary, Rutger et al. (1976) indicated that the sd-1 in a California mutant variety Calrose 76 (tentatively designated as sd-1p) reduces plant height by ca. 25% : this rate does not differ much when expressed in terms of culm length, much less than that of sd-1p (or sd-1h) which was estimated in this study. Such a comparatively great difference (10%) in estimated value of reduction effect between sd-1p by Rutger et al. (1976) and sd-1p (or sd-1h) by us might be attributable to the difference in genotypic value itself as well as the differences in genetic background and growing condition. If this is true, sd-1p (or sd-1h) and sd-1p will be different alleles at sd-1 locus. With this respect, further analysis will be needed.

In this study, it was also verified that Gimbozu has a semidwarfing gene (tentatively designated as sd(t)) non-allelic to sd-1. From Tables 3 and 5, sd(t) is assumed to reduce culm length by ca. 20%, much less than sd-1h. Gimbozu had often been used as a cross parent in practical rice breeding in Japan. There are a number of varieties derived from Gimbozu such as Koshihikari and Sasanishiki, and many of these varieties have a culm length almost equivalent to that of Gimbozu; hence, it seems that sd(t) is widely distributed among Japanese rice varieties and have played an important role in Japanese rice breeding.

HS90 has a remarkably short culm length (ca. 50 cm), harboring two semidwarfing genes. Such a short culm variety can not be found among the improved commercial varieties. On the basis of yielding-ability and harvest index, the optimum culm length of Japanese rice under the present cultivation methods is estimated to be around 70-80 cm, while that of modern indica varieties is estimated to be around 80-100 cm (Ashraf et al. 1993). Longer culm length is disadvantageous in terms of lodging and having greater respiration, thereby bringing forth low grain yield (Hayashi 1972). On the contrary, shorter culm length generally reduces grain yield, inevitably decreasing the total biomass production. These two genes, therefore, can not be used together in usual rice breeding aiming at raising excellent homozygous varieties.

In China, hybrid rices are planted in as many as about 13 million ha. covering about 40% of the total rice area today (Yuan and Virmani 1991). Also in Japan, several hybrid varieties have been released recently, though they have not yet been planted economically. Thus, the breeding of hybrid rices has become one of the most important subjects in rice breeding. It has often been pointed out that F1 hybrids, especially indica-japonica hybrids, tend to show a long culm length when compared with usual semidwarf varieties (Araki 1989). In this study, it was recognized that the F1 plants derived from Gimbozu (Sd-1 Sd-1 sd(t) sd(t)) × HS90 (sd-1b sd-1b sd(t) sd(t)) exhibited a culm length (68 cm : Fig. 2) almost equivalent to that of Jukkoku (71 cm : Fig. 3, 69 cm : Fig. 4), coming within the category of semidwarfism. This suggests that Sd-1 sd-1b sd(t) sd(t) is one of the favorable genotypes of F1 hybrid varieties. In general, seed parent should have a shorter culm than pollen parent, because the difference in culm length increases the chance of outcrossing, thereby enhancing the efficiency of obtaining hybrid seeds (Athwal and Virmani 1972, Rutger and Carnahan 1981). In view of this point, the favorable genotypes of seed and pollen parents for obtaining F1 hybrid with the genotype of Sd-1 sd-1b sd(t) sd(t) would be sd-1h sd-1h sd(t) sd(t) and Sd-1 Sd-1 sd(t) sd(t), respectively. As described above, the genotype of Sd-1b sd-1b sd(t) sd(t) brings about a remarkable reduction of culm length disadvantageous to seed production: in fact the grain yield of HS90 is somewhat lower (5-7%) than that of the original variety. Nevertheless, the genotype of sd-1h sd-1h sd(t) sd(t) is favorable to seed parent, eventually preventing the F1 hybrids from lodging.
Literature Cited


